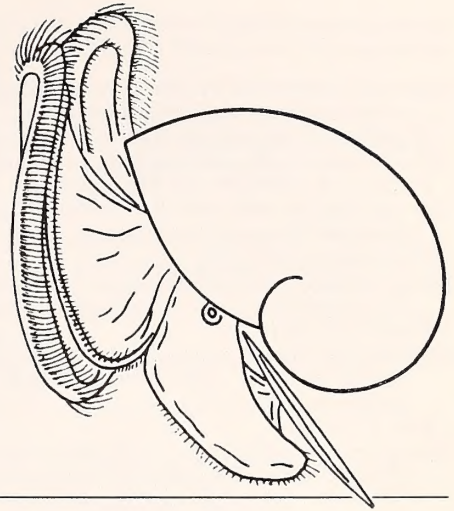


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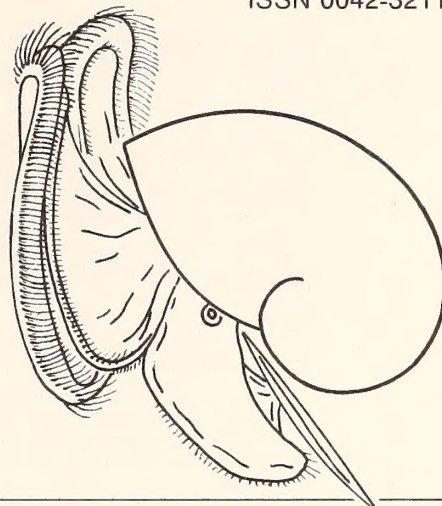
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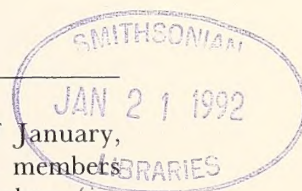
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THE VELIGER

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The Veliger is open to original papers pertaining to any problem concerned with mollusks.

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Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Phenotypic Plasticity in the Life Histories and Production of Two Warm-Temperate Viviparid Prosobranchs

by

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Abstract. Although prosobranch gastropods are common in southeastern rivers, little is known of the degree of phenotypic plasticity that occurs in their life histories and production ecology. We therefore studied cohort dynamics, life-history variation and secondary production in two viviparid prosobranchs at two sites in southern Louisiana. Bayou Manchac (BM), a slow-flowing flood-plain river, had levels of coarse and fine particulate organic material (potential food resources) twelve and six times greater, respectively, than did Old River (OR), an ox-bow lake, but also had lower average water temperatures, dissolved oxygen levels, pH, and water hardness. Considerable phenotypic plasticity in life histories and production occurred in both species. *Viviparus subpurpureus* (Say, 1829) dies after reproducing at an age of two years at BM, but grows more rapidly, reaches greater individual sizes, and reproduces and dies after only one year at OR. *Campeloma decisum* (Say, 1816) females reproduce at an age of two years, and then reproduce again and die at an age of three years at BM, but also grow more rapidly, reach larger shell lengths, and have an annual life-history pattern at OR. Females of both species at any given size brood more young at BM, but average clutch size is similar because females reach larger shell lengths at OR. Both species reached densities on the average four times higher at BM, resulting in higher annual standing stocks and greater annual production. Annual turnover rates, however, were two times greater at OR because of shorter development times and life cycles. Both snail species were found in deeper water at BM (with lower levels of dissolved oxygen) than at OR, suggesting that these snails are well adapted to hypoxia. When sub-adults of *V. subpurpureus* from both sources were reared at BM, differences in growth rates and numbers of embryos brooded disappeared, indicating that this intraspecific life-history variation is eco-phenotypic. We suggest that high levels of food resources at BM may promote greater fecundity, population density, and secondary production, but that lower temperatures and dissolved oxygen levels at the same habitat during summer may limit individual growth and result in longer life cycles in both species.

INTRODUCTION

Populations can often diverge considerably in life-history tactics, and the "ecological templet" (*e.g.*, environmental variables that alter or constrain phenotypic expression) is often important in explaining intraspecific variation (see review in PARTRIDGE & HARVEY, 1988). For example, in freshwater pulmonate snails such "eco-phenotypic" vari-

ation can be considerable (RUSSELL-HUNTER, 1978; McMAHON, 1983), and important environmental variables include periphyton quantity (EISENBERG, 1966; BROWN, 1985) and quality (EISENBERG, 1970; McMAHON *et al.*, 1974), population density (EISENBERG, 1970), and physico-chemical variables such as water temperature, dissolved oxygen, calcium concentration, and current velocity (McMAHON, 1983; LAM & CALOW, 1989).

Freshwater prosobranch snails also have considerable potential for eco-phenotypic life-history variation. First of all, they can have reduced tolerance adaptation to temperature, and greater sensitivity to temperature than pul-

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monates (*e.g.*, greater Q_{10} values, McMAHON 1983). Because they cannot rely on aerial respiration, as pulmonates can, and are oxyconformers (*i.e.*, show little regulation of oxygen consumption), they may also be more sensitive to hypoxia than are pulmonates (McMAHON, 1983). Viviparid prosobranchs also show a variety of feeding mechanisms that could promote increased phenotypic variation, including grazing on periphyton, deposit feeding, and even filter feeding (ALDRIDGE, 1983). Finally, viviparids may show greater levels of population divergence because, unlike pulmonates, which are passively dispersed by birds, viviparids are limited to the relatively poor dispersal abilities of adults along river systems (CLARKE, 1981; DAVIS, 1982). Prosobranch populations in separate drainage basins are therefore isolated, and speciation seems to have occurred at greater rates than in pulmonates (RUSSELL-HUNTER, 1978; DAVIS, 1982). For example, studies of electrophoretic variation in riverine prosobranchs indicate high levels of genetic variation among populations (CHAMBERS, 1980; DILLON & DAVIS, 1980; see review in BROWN & RICHARDSON, 1988).

Divergence in population characters may also alter energy flow through snail populations. Estimates of secondary production and biomass turnover are tightly linked to life-history traits (WATERS, 1979; BENKE, 1984). Thus, environmental variables affecting phenotypic expression of prosobranch life-history traits may also lead to variation in annual population production and P:B (production to biomass) ratios. Understanding intraspecific life-history variation is thus necessary to understand differences in production that exist among populations.

Little is known, however, about the degree of intraspecific life-history or production variation exhibited by southeastern populations of any prosobranch species, despite the fact that the southeastern United States is a center of diversity for the group (CLARKE, 1981; BURCH, 1982). Most recent studies of the life histories of viviparids have, for example, dealt with lentic populations in either the northeastern or midwestern United States (BROWN, 1978; JOKINEN *et al.*, 1982; PACE & SZUCH, 1985; BUCKLEY, 1986) or in Europe (RIBI & GEBHARDT, 1986; GEBHARDT & RIBI, 1987) and, for the most part, have not included production estimates. Two viviparid species, *Viviparus subpurpureus* (Say, 1829) and *Campeloma decisum* (Say, 1816), are common in tributaries of the southern reaches of the Mississippi River (BURCH, 1982) and have received some attention (BROWN *et al.*, 1989; RICHARDSON & BROWN, 1989); they are suitable subjects for such a comparative study.

Our purpose here is to delineate the range of intraspecific variation occurring in both species at two sites in southern Louisiana that differ markedly in several abiotic factors, including detrital abundance (a possible food resource, ALDRIDGE, 1983), water temperature, hardness, and dissolved oxygen saturation. We report differences in snail density through time, differences in individual growth

and cohort dynamics, female reproductive rates, and secondary production and P:B ratios for each species. We also compare the depth distributions of snails at each site, to determine if these snails are limited to shallow depths by hypoxic conditions in deeper waters. We also perform a "common garden" experiment, where sub-adults from both populations of one species are reared together at one site, to determine if life-history differences will disappear, suggesting that the variation is eco-phenotypic. Finally, we speculate on the relative importance of different ecological causes of the variation.

METHODS

Description of Habitats

Bayou Manchac (BM, also known as the Iberville River) flows through Baton Rouge, Louisiana, and is a tributary of the Amite River, which flows into Lake Maurepas. It has an extremely low gradient and slow flow, is approximately 10 m wide, varies from 3 to 6 m in depth, and has a clay substrate with a median particle size of 0.01 mm. It is surrounded with a rich riparian forest, which provides abundant allochthonous detritus each winter. Average wet mass of coarse organic detritus (defined as that retained on a 1.0-mm sieve) was $6.02 \text{ kg/m}^2 \pm 0.40$ (standard error of the mean, $n = 88$). Average fine organic content of the remaining sediment (estimated by ashing aliquots of sediment at 550°C overnight) was $5.7 \pm 0.6\%$ ($n = 21$). Average water temperature recorded over the sampling interval (October 1986 to October 1988) was $24.4^\circ\text{C} \pm 1.8^\circ\text{C}$ (maximum recorded was 28°C) and average dissolved oxygen level was $2.3 \text{ mg/L} \pm 0.5$, with a minimum of 0.5 and a maximum of 3.5 mg/L. Average water hardness was $68.3 \pm 9.9 \text{ mg/L}$ ($\text{Ca}^{++} + \text{Mg}^{++}$) and the average pH was 6.8 ± 0.1 . The sampling site was near the overpass of Highway 61 in southeastern Baton Rouge.

Old River (OR, also known as Lake Raccourci) is an ox-bow lake 90 km northwest of Baton Rouge. The ox-bow is connected via a channel to the Mississippi River, and water-level changes are frequent, retarding the growth of trees near the shoreline, and limiting allochthonous input. Average coarse organic detritus was only $0.43 \text{ kg/m}^2 \pm 0.04$ ($n = 59$), and percent fine organic content only $0.9 \pm 0.1\%$ ($n = 17$). The absence of a riparian canopy resulted in a much higher average water temperature (mean equal to $28.4 \pm 1.9^\circ\text{C}$, maximum recorded was 35°C). Dissolved oxygen values were at or near saturation at all sampling dates at OR (mean equal to $9.9 \text{ mg/L} \pm 0.6$). Average water hardness was much greater at OR (mean equal to $175.9 \pm 29.7 \text{ mg/L}$), as was pH (mean equal to 8.6 ± 0.2). At the sampling site, a sand bar along the north shore of the lake, 90% of the sediment particles were greater than 0.25 mm in diameter.

Voucher specimens for each species and site have been deposited at the Los Angeles County Museum of Natural

History: *Viviparus subpurpureus* from BM (LACM 91-103.1) and from OR (LACM 91-104.1) and *Campeloma decisum* from BM (LACM 91-103.2) and from OR (LACM 91-104.2).

Sampling Methods

Both sites were sampled approximately monthly during the summer, but less frequently during winter periods of high water, from fall 1986 (BM) or spring 1987 (OR) to fall 1988. At each date, 10 replicate samples were taken with a 15-by-15-cm Ekman grab. Ten replicate samples were enough for standard errors to be approximately 20% of the mean for snail densities, an acceptable level for benthic studies (ELLIOT, 1976). Counts of snails were converted to densities per m². Samples were sorted through a series of sieves (smallest diameter = 1.0 mm), and the snails removed and sorted to species, with individual shell lengths determined to the nearest 0.1 mm using a caliper. A 1.0-mm sieve retained all snails because embryos are released at sizes ≥ 3 mm (BROWN *et al.*, 1989).

Life-History Traits and Secondary Production

Size-frequency histograms were used to follow cohorts and estimate life-cycle length and individual growth rates. We approximated life-cycle length by determining the period of time between the appearance of juveniles and disappearance of adults in cohorts, and assumed individual growth rates were similar to changes in the median shell size of cohorts through time. To estimate population sex ratios, as well as the size that males and females reached in each population, approximately 30 randomly selected snails (for each species and site) were dissected at each sampling date and sexed, and the number of embryos brooded in each female recorded. Male viviparids are easily distinguished by their larger right tentacle, which is used in copulation. For a subset of these animals, adult dry tissue masses (including eggs in females) were determined on an analytical balance (sensitivity = 0.1 mg) after drying overnight at 60°C. A two-way ANOVA (sex versus site) was performed for each species to detect any site-dependent effects on, or sexual dimorphism in, shell length and dry body mass.

For the estimation of secondary production, regressions of snail shell-free dry mass versus shell length were used to estimate sample standing stocks from the shell size-frequency distributions in samples (see discussion of methods in RICHARDSON & BROWN, 1989). We then multiplied these size-specific dry masses times the density of the size classes in samples to calculate total snail biomass/m². Regressions of dry tissue mass versus shell length had coefficients of determination (r^2) ranging from a low of 0.74 ($n = 50$) for *Campeloma decisum* at OR to a high of 0.88 ($n = 50$) for *C. decisum* at OR. Production was estimated with the size-frequency method (HYNES & COLEMAN, 1968; HAMILTON, 1969) as modified by KRUEGER & MARTIN

(1980). Production estimates include embryo dry mass (see methods in RICHARDSON & BROWN, 1989), and are corrected for cohort production interval (CPI, BENKE, 1979) and unequal sampling intervals (KRUEGER & MARTIN, 1980). Negative production values for smaller size classes are not included in the overall estimate, following BENKE (1984).

Depth Distributions

At two separate dates for each site during summer 1989, we determined the vertical distribution of temperature and dissolved oxygen using a YSI meter, and then collected three replicate samples at 0.5, 1.5, and 2.5 m depth at each site. These depths were selected because the maximum depth of BM in summer 1989 was approximately 3 m. Samples were processed as discussed above, and the log-transformed (to remove a mean-variance correlation) densities of both species were subjected to a two-way ANOVA at each site to determine, for each species, the effect of sampling date and depth on abundance.

Field Growth Experiment

Finally, we performed a field experiment to determine if life-history differences between sites in one species had a strong genetic component, or were due more to such environmental differences as food levels. This experiment was performed in BM from April to September 1988, with *Viviparus subpurpureus*. Sub-adults (15.0 ± 1.0 mm initial mean shell length) from both source sites were held at representative field densities in cages at the sampling site in BM. We determined the average shell length and wet total mass (shell plus tissue) attained by snails at the end of the experiment, and compared them between the two source populations with *t*-tests to determine any differences in growth. We also dissected all females to determine any differences in brood size.

Cages were plastic trays ($52 \times 63 \times 11$ cm, with a bottom surface area of roughly one-third m²), similar to bread storage trays used in bakeries (Allibert Industries, Quebec, Canada). They were made of impact resistant plastic, open at the top, and had mesh sides and bottoms with openings 5×5 cm. The trays were covered and lined with plastic mesh (mesh diameter 2 mm) hot glued to the trays to retain all snails, including embryos. Trays were placed at approximately 0.5 m depth (the depth at which most of the previous sampling occurred), and were allowed to settle into the clay substrate so that detritus would be available to the snails.

RESULTS

Density

Both species were roughly four times as abundant, on the average, at BM than at OR (Figure 1). For *Viviparus subpurpureus*, populations declined to lows of about 100

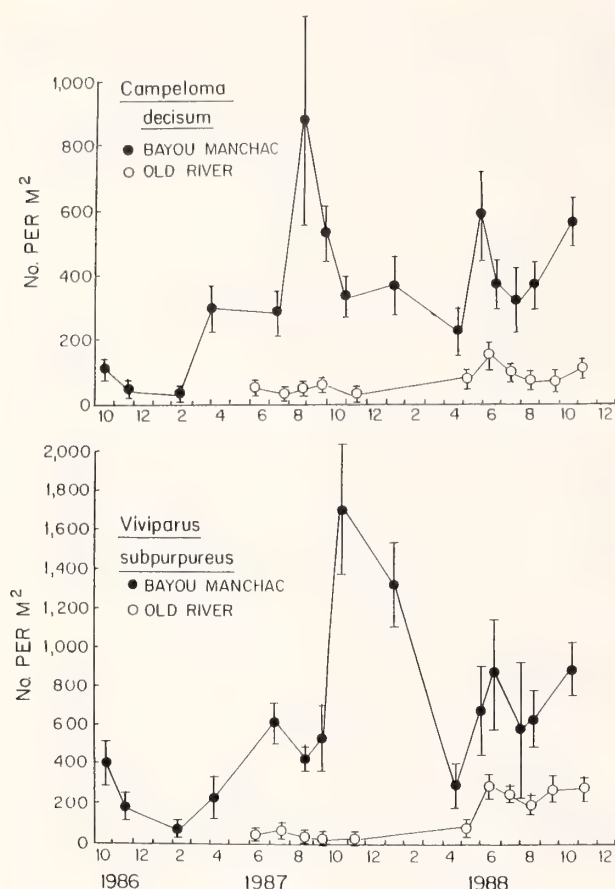


Figure 1

Temporal changes in the density (\pm SE, $n = 10$) of *Viviparus subpurpureus* and *Campeloma decisum* at two warm-temperate sites in southern Louisiana.

to 300 snails/m² after winter floods (BROWN *et al.*, 1989), but reached densities as high as 1700/m² after recruitment of embryos in the summer. Corresponding densities at OR ranged from 50 to 250/m². To determine whether abundances differed significantly between sites, we performed a one-way ANOVA with each site and date combination as a separate treatment. Densities were log transformed to remove a mean-variance correlation. Using an orthogonal contrast, we found that *V. subpurpureus* was significantly more abundant at BM ($F = 135.3$, $P < 0.001$). For *Campeloma decisum*, densities at BM ranged from 30 to 850/m², versus peak densities of only 150/m² at OR. A similar one-way ANOVA with an orthogonal contrast between sites revealed these densities to again be highly significantly different ($F = 50.6$, $P < 0.001$).

Cohort Dynamics and Life-History Variation

At BM, adult *Viviparus subpurpureus* produced a large cohort of juveniles during March and April 1987 (Figure 2). By October, these snails had reached a mean shell

length of 13 mm. Since juveniles are released at 3 mm shell length, this represents a growth rate of 1.43 mm per month (e.g., a 10-mm increment over seven months). Mean shell length of this same cohort eventually reached 20 mm in fall 1988, when the snails had reached an age of one and a half years. Some of the original adult cohort probably survived until the fall of 1987, but most died after reproducing, explaining why there are few snails in the size classes of 16 to 26 mm during the last six months of 1987 (Figure 2).

When sampling began at OR in spring 1987 (Figure 3), *Viviparus subpurpureus*, probably born earlier that spring, averaged 13 mm in shell length, or about 3 or 4 mm longer than the corresponding cohort in BM. These snails had reached an average shell length of 23 mm by fall 1987, or 10 mm greater than the corresponding cohort in BM. Some juveniles were born to this cohort in fall 1987, but a major release of juveniles occurred just before the first sampling in 1988, probably in April. These snails had again grown to an average size of 23 mm by fall 1988, for an average growth rate of 2.86 mm per month (20-mm increment in seven months) or roughly twice the growth rate in OR. Either these snails, or some surviving older adults, had started releasing embryos by fall 1988 (Figure 3).

The sex ratio of *Viviparus subpurpureus* was biased towards females at BM (χ^2 test, $n = 275$, $P < 0.01$) but not at OR ($n = 212$, $P = 0.07$). Female *V. subpurpureus* at both sites had significantly greater shell lengths (Table 1, $P < 0.0001$) and body dry tissue masses (Table 1, $P < 0.001$) than did males. The greater average tissue masses of females could be due, however, to the embryos they were holding, since embryos were included in these estimates. *Viviparus subpurpureus* also reached greater average shell lengths ($P < 0.0001$) and body dry masses ($P < 0.001$) at OR than at BM.

Females started brooding young at a shell length of 16 mm at BM versus a shell length of 19 mm at OR. Clutch-size versus shell-length regressions had similar slopes ($P > 0.05$) but significantly different intercepts ($P < 0.0001$) indicating that female *Viviparus subpurpureus* at any shell length in BM were brooding more embryos than equivalent OR females. However, the larger female size at OR explains why females did not differ significantly in mean clutch size between sites (about 10 embryos per female at each site, $P > 0.05$).

Campeloma decisum produced a large cohort of juveniles in March 1987 at BM (Figure 4), and these snails had reached an average size of 15 mm by October, for an average growth rate of 1.71 mm per month (12-mm increment in seven months). This cohort reached a maximum shell length of about 20 mm in late 1988 at an approximate age of one and a half years. A second cohort, born in April 1988, had reached a size of 12 mm by October 1988, with an average growth rate of 1.29 mm per month (e.g., 9-mm growth increment divided by seven months). Some snails from the original cohort of adults seen in fall

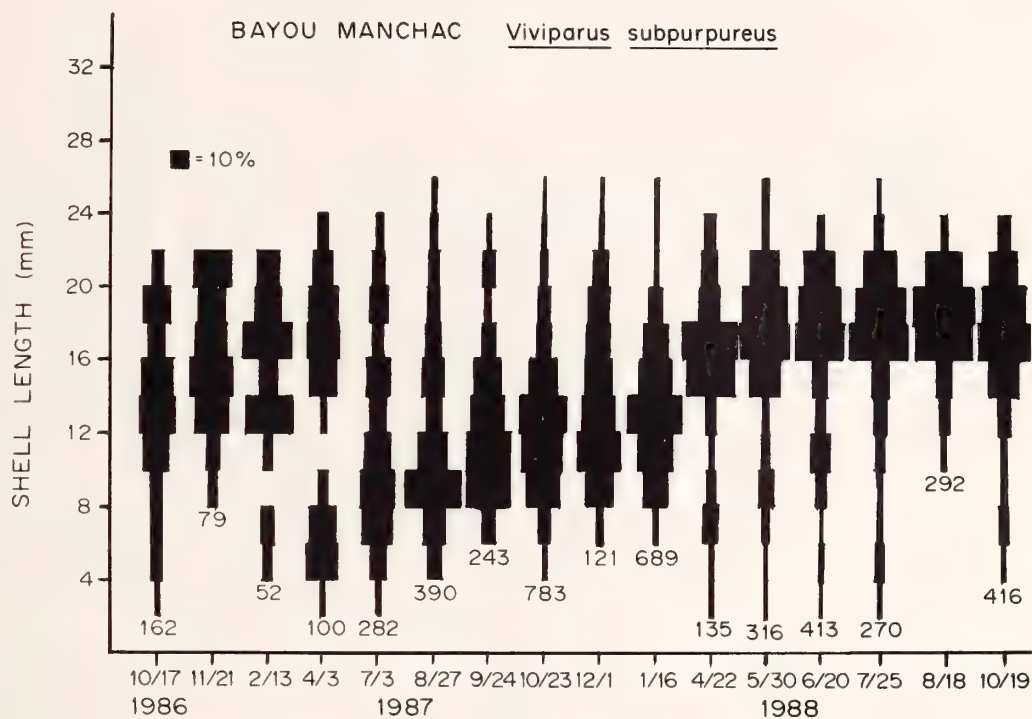


Figure 2

Percentile size-frequency histograms for cohorts of *Viviparus subpurpureus* at Bayou Manchac. Sample sizes are given below histograms, and sampling dates are given on the x-axis.

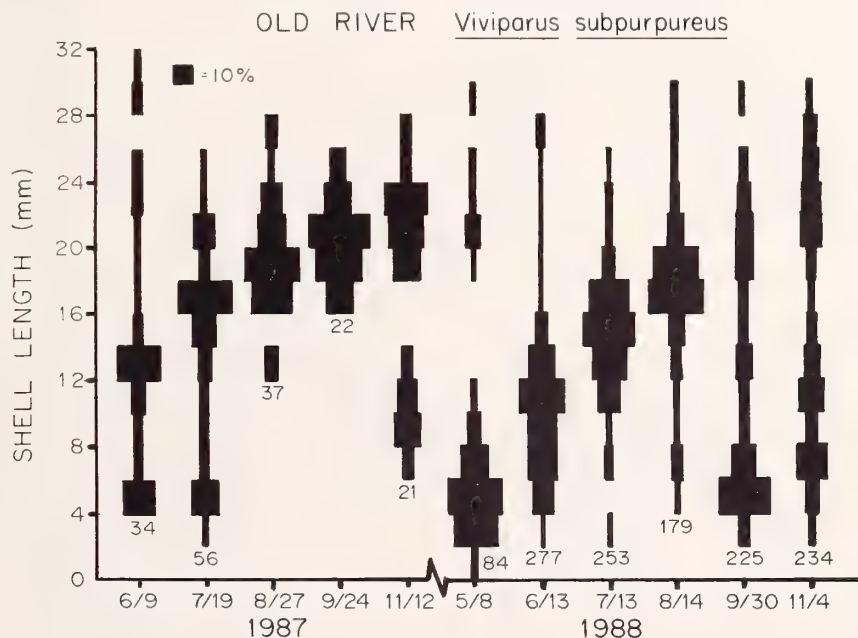


Figure 3

Percentile size-frequency histograms for cohorts of *Viviparus subpurpureus* at Old River. Sample sizes are given below histograms, and sampling dates are given on the x-axis.

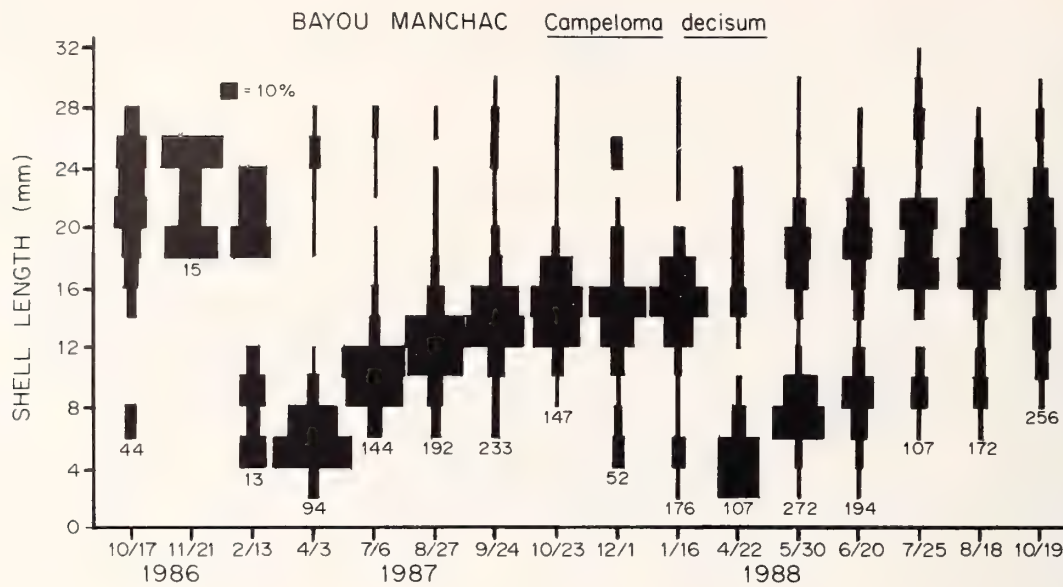


Figure 4

Percentile size-frequency histograms for cohorts of *Campeloma decisum* at Bayou Manchac. Sample sizes are given below histograms, and sampling dates are given on the x-axis.

1986 were found in samples as late as mid-summer 1988. Because in 1986 these snails averaged the same size as one-and-a-half year olds in fall 1988 (e.g., 20 to 24 mm, Figure 4), they would be three years old in summer 1988.

At OR, two cohorts of *Campeloma decisum* were present in June 1987 (Figure 5). The younger cohort grew from about 8 mm shell length in June to 16 mm by November, merging with the older cohort. This combined cohort survived the winter, and produced a large cohort of juveniles just before sampling started (again delayed due to high waters) in spring 1988. Assuming these young were produced in April, and since they reached an average size of

18 mm by November 1988, growth rates would average 13 to 15 mm per seven months, or about 2 mm per month. Again, as in *Viviparus subpurpureus*, cohorts of *C. decisum* reached larger average sizes and appeared to have greater average growth rates at OR than at BM.

The sex ratio of *Campeloma decisum* was biased towards females at BM ($n = 226$, $P < 0.01$), but males at OR ($n = 198$, $P < 0.01$). Thus, three of the four populations had biased sex ratios, with females favored in both cases at BM, and sexes either equally abundant or males more common (in *C. decisum*) at OR. Female *C. decisum* reached greater shell lengths on the average than males (Table 1,

Table 1

Average life-history traits (\pm SE) for both sexes of *Viviparus subpurpureus* and *Campeloma decisum* at both sites, determined by dissecting individuals sampled from the field. Sample sizes are given in parentheses. Note that only a subsample of snails had shell and body dry masses determined.

Site	Sex	<i>Viviparus subpurpureus</i>		<i>Campeloma decisum</i>	
		Shell length	Body mass	Shell length	Body mass
Bayou Manchac	female	18.8 \pm 0.2 (n = 182)	98.2 \pm 3.3 (n = 92)	20.1 \pm 0.4 (n = 168)	106.6 \pm 6.6 (n = 84)
	male	15.6 \pm 0.2 (n = 93)	63.7 \pm 3.8 (n = 54)	16.8 \pm 0.5 (n = 58)	82.7 \pm 10.7 (n = 20)
Old River	female	21.1 \pm 0.1 (n = 119)	114.0 \pm 9.8 (n = 48)	22.6 \pm 0.6 (n = 72)	79.1 \pm 12.6 (n = 22)
	male	19.0 \pm 0.4 (n = 93)	104.7 \pm 11.0 (n = 36)	21.4 \pm 0.3 (n = 126)	107.1 \pm 6.7 (n = 44)

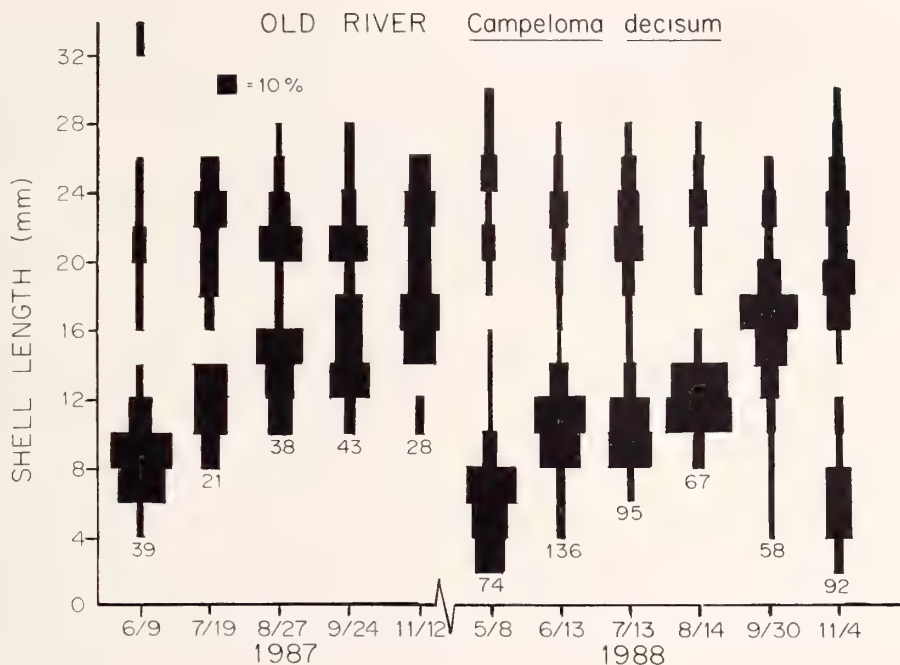


Figure 5

Percentile size-frequency histograms for cohorts of *Campeloma decisum* at Old River. Sample sizes are given below histograms, and sampling dates are given on the x-axis.

$P < 0.0001$) but not greater body dry tissue masses ($P > 0.05$), even though embryos were again included in female tissue mass. However, there was also a significant site \times sex interaction for shell length ($P < 0.05$), indicating that sexual dimorphism in shell length was more obvious at BM, as well as a significant interaction between sex and site for body mass ($P < 0.05$) with the effect of sex reversed between habitats (Table 1). Finally, *C. decisum* had significantly greater shell lengths at OR (Table 1, $P < 0.0001$) but not greater dry body tissue masses ($P > 0.05$) than at BM.

At Bayou Manchac, female *Campeloma decisum* start brooding embryos at shell lengths of 19 mm, compared to 21 mm at Old River. Clutch size also increases more rapidly with shell length at BM than at OR ($P < 0.001$). Thus the larger females at OR again do not have significantly greater average clutch sizes (about 12 embryos per female at each site).

Secondary Production

These density, life-history, and growth-rate differences among populations can be summarized easily by comparing annual secondary production, which in one value integrates density, life-cycle length, reproductive patterns, and growth (BENKE, 1984). Production was significantly higher (comparing 95% C.I.) for *Viviparus subpurpureus* at BM than at OR, primarily because of higher biomass levels (Table 2). Even though growth rates were greater

at OR, lower average biomass resulted in a 79% decrease in production between sites. Complete turnover of biomass, however, occurred almost two times faster at OR, reflecting faster individual growth at this site (Table 2). For *Campeloma decisum*, both production and biomass were also dramatically lower at OR, again because greater growth rates were counterbalanced by lower annual biomasses. Turnover rates (P:B ratios) were again about twice as great at OR (Table 2).

Table 2

Annual production (P) and mean biomass (B) in grams of shell-free dry mass/m², and P:B ratios for *Viviparus subpurpureus* and *Campeloma decisum*. Estimates were calculated using the size-frequency method. 95% confidence intervals are in parentheses.

	Bayou Manchac	Old River
<i>V. subpurpureus</i>		
P	81.8 (19.0)	17.2 (5.9)
B	32.3 (8.2)	4.0 (1.7)
P:B	2.5	4.3
<i>C. decisum</i>		
P	31.3 (7.42)	11.1 (5.7)
B	15.5 (4.6)	2.7 (1.9)
P:B	2.0	4.1

Table 3

Comparison of reproductive performance for two source populations of *Viviparus subpurpureus* reared at Bayou Manchac in cages; see text for methods. Sample sizes are in parentheses.

Trait	Source		P*
	Bayou Manchac	Old River	
Mean final shell length (mm)	18.9 ± 0.2 (55)	18.3 ± 0.4 (20)	>0.05
Mean final total mass (mg)	1767.0 ± 59.0 (55)	1598.0 ± 96.0 (20)	>0.05
Brood number	14.5 ± 1.2 (49)	13.6 ± 2.2 (15)	>0.05

* Significance of *t*-test.

Depth Distributions

Both BM and OR are relatively shallow habitats, and neither stratified thermally during summer 1989. However, OR had temperatures averaging 3°C greater than those at BM on the first set of sampling dates, which were within two days of each other. This is due to lack of a riparian shade cover at OR. A substantial difference also occurred in dissolved oxygen profiles, with BM values averaging only 18% of saturation versus 122% at OR. Vertical stratification of dissolved oxygen was more pronounced at both sites on the second sampling date. At BM, there was no consistent relationship between the density of either *Viviparus subpurpureus* or *Campeloma decisum* and sampling depth ($P > 0.05$).

At OR, however, densities declined much more rapidly for each species with depth. While there was no significant difference in the density of *Viviparus subpurpureus* between dates, there was a highly significant effect for sample depth ($P < 0.01$). Similarly, average densities did not differ between dates for *Campeloma decisum* ($P > 0.05$) but did among depths ($P < 0.01$).

Field Rearing Results

The results of the field rearing experiment (Table 3) indicated little difference in growth or reproductive per-

formance between snails from the two populations when *Viviparus subpurpureus* were held in a common environment (BM). Both average shell length and wet total mass (shell plus body) were very similar for individuals from the two populations at the end of the experiment (Table 3). Female brood sizes did not differ between the two populations either (Table 3). Since snails had initially similar sizes, we would have expected snails from OR to have reached larger sizes if the growth differences shown by this population were of genetic origin.

DISCUSSION

Life History Differences Among Sites

Considerable intraspecific variation occurred in life-history patterns of both species at both sites (summarized in Table 4). *Viviparus subpurpureus* reached dramatically greater abundances at BM, but individual growth rates were half those at OR, and both males and females reached smaller final adult sizes than at OR. The size-frequency histograms and dissections of females suggest that *V. subpurpureus* is biennial and semelparous at BM, but annual at OR. For example, because year-old females were only 14 mm long on the average at BM, and brooding did not start in this habitat until a shell length of 16 mm, females probably did not mature until an age of one and a half years, in their second fall. Furthermore, because a large cohort of juveniles was not produced in the fall, these females probably brooded their young over their second winter and released them in their third spring at an age of two years. In contrast females at OR reached sizes at which embryos were present in brood pouches by the end of their first summer (at an age of one-half year). These females may have released some young (a few juveniles were present in the fall), but most females probably brooded embryos over their first winter, and released them in the spring at an age of one year, dying shortly thereafter.

Campeloma decisum also reached higher densities at BM, but again had individual growth rates, about 55% greater, at OR (Table 4). Size-frequency histograms and dissections also suggest that *C. decisum* is biennial and semel-

Table 4

Summary of the relative magnitudes of average physico-chemical and demographic variables for the two viviparid species at two sites in Louisiana.

Variable	Bayou Manchac	Old River
Detrital abundance	6x	x
Water temperature	x	x + 4°C
Dissolved oxygen	28% saturation	128% saturation
Water hardness	x	1.3x
Snail densities	ca. 4x	x
Life-cycle lengths	ca. 2x	x
Individual growth	x	ca. 1.5–2x
Production	ca. 3–5x	x

parous, or even triennial and iteroparous at BM, but annual and semelparous at OR. For example, females at BM evidently do not reach a shell length where they can brood young (18–19 mm) until their second fall, when they are one and a half years old. Thus they probably brood their young over the winter and release them in spring, at an age of two years. A fraction of these females, judging from the size-frequency histograms, may survive and reproduce in a third year. In contrast, females at OR have reached a size where they can brood young by the end of their first summer (at an age of one-half year), and probably brood embryos over the winter, releasing them the next spring. The size-frequency histograms indicate that some females may survive to the end of summer, for a life-cycle length of one and a half years.

These life-history differences between BM and OR populations of both species are also reflected in the production data (Table 4). Because of the higher densities, standing stocks and production were considerably greater at BM for both species. The magnitude of production depends both on standing stocks and the annual P:B ratio (BENKE, 1984), and higher production at BM was thus apparently the result of higher standing stocks. Disparity in production and biomass estimates are not uncommon between molluscan populations, and these differences for *Viviparus subpurpureus* and *Campeloma decisum* fall within the observed range (see review in RUSSELL-HUNTER & BUCKLEY, 1983).

However, annual turnover ratios (P:B ratios) were approximately twice as high at OR for both *Viviparus subpurpureus* and *Campeloma decisum*. Because turnover ratios are dependent on development times (WATERS, 1979; BENKE, 1979) and are also inversely related to the length of the life cycle (RUSSELL-HUNTER & BUCKLEY, 1983), it is understandable that annual P:B ratios were higher at the site with fastest growth and shortest snail longevity (OR). The P:B ratios for the annual populations at OR are within the range of 2.1–9.2 reported for other semelparous, annual snails. The BM populations, with somewhat longer life-spans, have ratios fairly similar to those reported for snails with triennial or biennial, semelparous populations (1.0–2.0, RUSSELL-HUNTER & BUCKLEY, 1983).

The life-history and production data are intriguing in comparison to other intraspecific studies of life-history variation in freshwater snails, for a number of reasons. First, the length of the life cycles, especially those at OR, are some of the shortest recorded for freshwater prosobranchs. A more typical pattern for north-temperate populations of viviparid prosobranchs is for females to mature (e.g., give birth to offspring) at the earliest at two years of age and to be semelparous, or in some cases to reproduce for several years (BROWNE, 1978; JOKINEN *et al.*, 1982; BUCKLEY, 1986; see ALDRIDGE, 1983, for a review). The densities recorded at BM are also much higher than densities recorded in even exceptionally abundant north-temperate populations (PACE & SZUCH, 1985). However, males

in these warm-temperate populations still reach smaller shell lengths and/or possibly have shorter life cycles, similar to the sexual dimorphism seen in more northern populations. The resulting high standing crops, as well as the short life cycles, result in secondary production estimates that are much higher than those for most north-temperate, gastropod populations (see review in RUSSELL-HUNTER & BUCKLEY, 1983), and indeed are some of the highest known for any lotic organism (see BENKE, 1984). Evidentially the warmer water temperatures, longer growing seasons, and/or greater food resources may explain the shorter life cycles, rapid growth, and greater productivity of these warm-temperate populations (RICHARDSON & BROWN, 1989).

The differences in growth rates and life-cycle lengths between habitats in this study are paradoxical in light of earlier studies. In north-temperate pulmonates and prosobranchs, increased food availability not only causes higher densities and secondary production, but also greater individual growth rates, shorter life cycles, and greater reproductive rates (see reviews in RUSSELL-HUNTER, 1978; McMAHON, 1983; ALDRIDGE, 1983). The higher densities and secondary production of both species at BM (the detritus-rich site) are as expected since *Campeloma decisum* is considered a detritivore or scavenger (PACE & SZUCH, 1985) and other species of *Viviparus* are known to deposit feed (see ALDRIDGE, 1983). The lower growth rates and longer life cycles at BM than at OR are, however, not as expected, and we consider potential causes below.

Potential Causes of Intraspecific Life-History Variation

We will first discuss those potential causes that seem less likely to be important. The intraspecific life-history variation in these populations does not appear to have a strong genetic basis, since life-history differences disappeared upon rearing individuals in a common environment. We consider the experiment a fairly conservative test, since the snails were actually sub-adults that had spent about a year in their source habitats before the experiment began. These data suggest that much of the variation is eco-phenotypic (*i.e.*, of ecological origin).

What then are the important ecological variables? McMAHON (1983) and ALDRIDGE (1983) reviewed the physiological ecology of pulmonates and prosobranchs, respectively, and listed a large number of studies suggesting that temperature, water hardness, and resource levels are important determinants of life-history variation. Of these, the least likely single factor in this study appears to be dissolved oxygen concentration. The lowest oxygen levels occurred at BM (Table 4), where population densities were highest. Furthermore, snails were distributed down to the greatest depths at BM. There was actually more of a decrease in density with depth at the more oxygenated site, OR. However, lower oxygen levels may still have affected the energy available for individual growth in the following way. If most of the respiration at BM was an-

aerobic, because of low oxygen levels, then the decreased efficiency of anaerobic metabolism might have significantly lowered the amount of non-respired, assimilated energy available for growth. Thus even with the greater food resources, snails at BM might have lower growth rates than snails at OR (if these snails were able to use aerobic respiration and to more efficiently convert assimilated energy into growth).

On the other hand, average water temperatures were also higher at OR (Table 4) during summer months because of the absence of a leaf canopy. Water temperature dramatically increases feeding rates and shell deposition, resulting in increased growth and shorter life cycles both in pulmonates (McMAHON, 1983) and prosobranchs (ALDRIDGE, 1983). In addition, OR has harder water (Table 4), which may also increase the rate of shell deposition. Thus the warmer, harder, and more oxygenated water at OR may synergistically promote more rapid growth rates. Furthermore, this explanation is not necessarily counter to the observed higher densities and fecundities for females (at any given shell length) at BM. During the winter months, when females are brooding embryos, differences in water temperature and oxygen concentration are not as large between the two habitats. The riparian vegetation along BM loses its leaves, allowing greater absorption of incoming solar radiation by the water, and lower water temperatures overall result in similar dissolved oxygen levels.

Two final environmental factors should be considered. First, the overall higher density of snails at BM may have resulted in a density-dependent reduction in individual growth rates, as has been recorded often in freshwater snails (e.g., among others, EISENBERG, 1970; HUNTER, 1975; BROWN, 1985). However, it is hard to understand why density-dependent reductions in fecundity, just as often if not more widely documented, would not occur as well. Finally, size-specific predation by crayfish can alter cohort size distributions, either by the preferential removal of smaller snails, or by causing snails to increase their allocation to growth versus reproduction (CROWL & COVICH, 1990). However, the crayfish *Procambarus clarkii* is common in BM, and is a voracious feeder on the young of both snail species (VARZA, 1989), suggesting that the growth-rate differences between the two habitats were not due to crayfish predation.

Regardless of the causal mechanisms, the eco-phenotypic variation in the life histories of these prosobranch snails has some important implications for prosobranch evolutionary biology. First, considerable phenotypic plasticity occurs in the life histories of these populations. Such plasticity is undoubtedly adaptive, since it allows responses to changes in environmental variation (see discussion in RUSSELL-HUNTER, 1978). In this study, for example, females of a given size at the site with apparently lower food resources (OR) did not brood as many embryos. By growing to a larger size, however, they could still produce an

equivalent number of offspring, conserving individual fitness.

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Multiple Paternity in *Crepidula fornicata* (Linnaeus)

by

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Abstract. The protandric hermaphrodite *Crepidula fornicata* (Linnaeus) is typically found in stacks containing individuals of both sexes as well as immature and transitional forms. Although multiple mating has been observed, it is not known whether it results in multiple paternity. Starch gel electrophoresis of mothers and their broods demonstrated effective sperm storage and multiple paternity, as well as genetic contributions by individuals not present in the stacks at the time of collection. In order for *C. fornicata* to be useful as a model system for studies of sex change in the Mollusca, the use of more powerful, currently available methods is recommended to elucidate the ecological dynamics of fertilization and paternity.

INTRODUCTION

The calyptraeid snail *Crepidula fornicata* (Linnaeus) is a protandric hermaphrodite in which the change from male to female is influenced by various biotic factors, making it a potentially useful model system for the study of strategies of sex allocation (HOAGLAND, 1978; CHARNOV, 1982; WRIGHT, 1988). In order to understand the evolution of such strategies, we must know more about the "ecological dynamics of fertilization and paternity" (WRIGHT, 1988). Two aspects of particular importance in the case of *C. fornicata* are (1) whether sperm are stored, and if so, for how long, and (2) whether multiple paternity is possible.

Although considerable indirect evidence indicates that many gastropods may store sperm for long periods, this phenomenon has not been studied in detail in prosobranchs. COE (1942) reported that *Crepidula onyx* was capable of storing sperm for more than a year; a similar observation was made by HOAGLAND (1978) for *C. fornicata*. Evidence for multiple paternity in prosobranchs is likewise anecdotal, but it has been reported in several pulmonates (MURRAY, 1964; MULVEY & VRIJENHOEK, 1981). COE (1936) described multiple insemination of a single female *C. fornicata* by several young males, and noted that young males "often attach themselves to the sides of groups as 'supplementary' males or settle down singly on other objects after having presumably participated in temporary matings with one or more females" (COE, 1938).

ORTON (1950) reported that copulation took place between individuals occupying any position in a chain; on the other hand, WILCZYNSKI (1955) argued that copulation in stacks was severely restricted, with motile males probably siring the majority of offspring. ORTON (1952) provided circumstantial evidence to suggest that isolated individuals may be self-fertilized by their own sperm upon transition to the female phase, but this hypothesis has yet to be tested experimentally.

Our understanding of the ecological dynamics of fertilization and paternity in *Crepidula* is limited at present by a lack of empirical data. We report here the occurrence, detected by allozyme electrophoresis, of multiple paternity in a natural population of *C. fornicata*.

METHODS AND MATERIALS

Crepidula fornicata were collected intertidally at Cape Henlopen, Delaware, in July 1988. For each substrate (*i.e.*, a single rock, shell, or other hard object), all snails (one "substrate group") were removed and labelled individually according to substrate, stack, and position in a stack. Sex was determined by examination of gross morphology under a dissecting microscope. Several stacks were dismantled, and females brooding larvae were placed in individual 4-L glass jars containing filtered seawater, where they remained until most or all of the larvae were released. The adults were then removed from the jars, and the larvae were fed daily with a mixture of *Isochrysis galbana* and *Chaetoceros calcitrans*. Larvae were cultured from a single brooding female from each of six substrate groups. Adults

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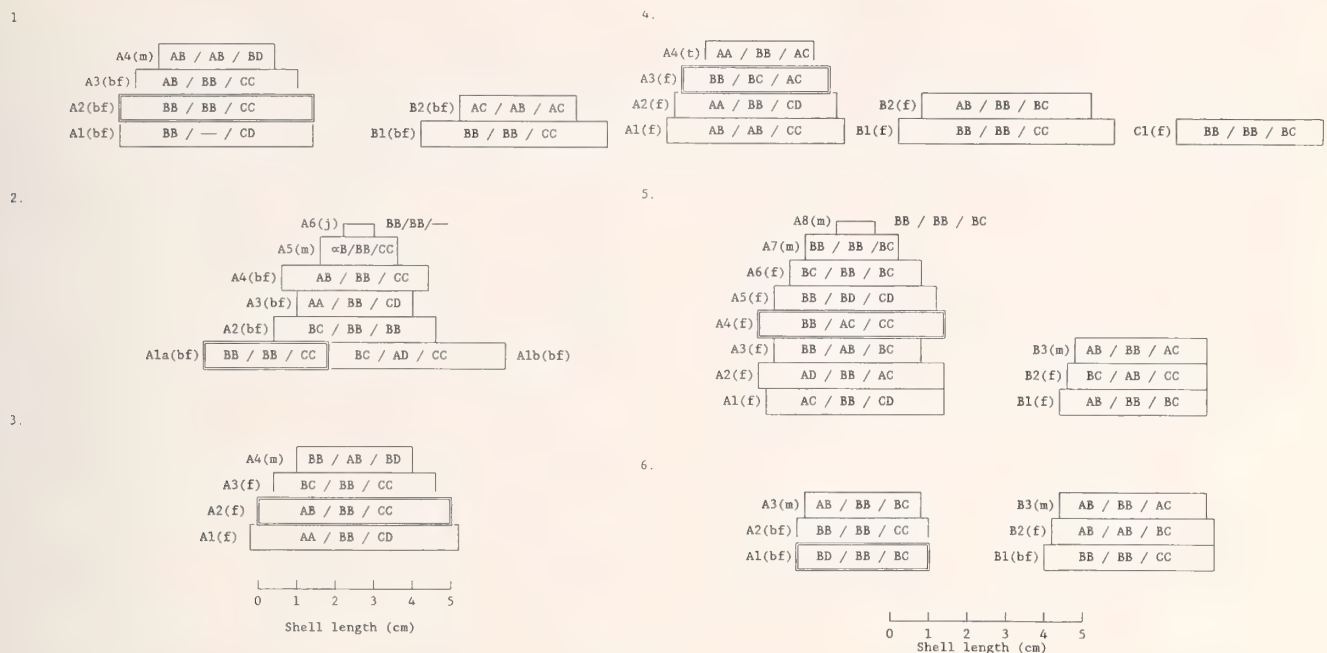


Figure 1

Diagrams of six substrate groups showing stack composition and genotypes at three enzyme-coding loci (*Gpi/Mpi-2/Pgm*). "—" indicates genotype not obtained. Individual snails are indicated by boxes, with shell length drawn approximately to scale indicated. Key: f, female; bf, brooding female; m, male; t, transitional; j, juvenile. Brood status of females in groups 4 and 5 was not recorded. Double lines mark the female whose brood was sampled.

were held in the laboratory for approximately one week before being stored at -76°C for electrophoresis.

All adults and a random sample of juveniles from each brood (when they had reached a minimum size of 4–6 mm) were homogenized in equal volumes of 0.1 M Tris pH 8.0 buffer containing 20% glycerol. After centrifugation at 5000 *g* for 5–10 min a portion of the supernatant from each sample was loaded onto starch gels. Several enzyme systems were stained: glucose phosphate isomerase (GPI, E.C. 5.3.1.9), mannose phosphate isomerase (MPI, E.C. 5.3.1.8), phosphoglucosyltransferase (PGM, E.C. 2.7.5.1), and nonspecific esterases hydrolyzing the fluorescent substrate 4-methylumbelliferyl acetate. Enzymes that were scored reliably in both adults and juveniles were GPI, MPI, and PGM. Three regions of esterase staining (putative loci) were inconsistently scored in the progeny but were not resolved in adults. All enzymes were run on the discontinuous lithium hydroxide pH 8.4 buffer of SELANDER *et al.* (1971) except for PGM, which was run on the 0.18 M Tris-borate-EDTA pH 8.7 buffer of BOYER *et al.* (1963). Alleles were designated alphabetically (A to D, in order of decreasing electrophoretic mobility). For two loci, *Gpi* and *PGM*, a faster-migrating electromorph was discovered later and called α .

The initial null hypothesis was that each brood had been sired by the individual located directly above the brood mother. If the array of progeny genotypes led to the rejection of this hypothesis, we next asked whether an

individual located higher in the stack (or one in another stack in that substrate group) could have sired the entire brood. Rejection of this hypothesis implies either that more than one male contributed to a single brood, or alternatively that the responsible male was absent at the time of collection. In addition, we estimated our ability to detect sires not present in the stacks, by considering genotypic frequencies in the population at large. The latter were derived from a sample of 212 individuals obtained at the same time we collected the snails used for paternity analysis. For example, in substrate group 1, contributions by a male bearing a *Gpi* genotype other than AA, AB, or AB would have been evident, as would contributions from a male with a *Mpi-2* genotype other than AA, AB, or AB. The estimated frequency of individuals thus detectable by the use of these two loci is 23%, so in this case our ability to detect the contributions of visiting males to this brood was weak. In some cases (see below), our power of discrimination was better. Although this simple paternity exclusion procedure lacks the resolving power of studies employing either numerous polymorphic gene loci or hypervariable genes (DNA fingerprinting), it nevertheless proved capable of demonstrating multiple paternity.

RESULTS

The substrate groups and genotypic constitution of individual snails at three allozyme loci are depicted in Figure

Table 1.

Genotypes of progeny in broods from six females depicted in Figure 1. ND = no data.

Substrate group	Female	Progeny genotypes					
		<i>Gpi</i>	<i>Mpi-2</i>	<i>Pgm</i>	<i>Est-1</i>	<i>Est-2</i>	<i>Est-3</i>
1	A2	9 AB 7 BB	7 AB 9 BB	ND	ND	9 BB 3 BC 2 CC	ND
		37 AB					
2	Ala	3 BB 1 BC	3 AB 41 BB	ND	ND	3 AB 33 BB	15 BB
		17 AB					
3	A2	6 BB 1 BC	7 AB 15 BB	4 BC	9 AA	ND	15 BB
4	A3	14 BB 5 BC	4 AC 4 CC	4 AC 4 CC	2 AB 5 BB	ND	13 AB 10 BB
		23 AB					
5	A4	2 AB 13 BB 1 BC	6 AB 10 BC	12 BC	11 AA 6 AB 1 BB	ND	9 BB
		10 AB					
6	A1	3 AD 12 BB 7 BD	33 BB	7 BB 10 BC	4 AA 7 AB 3 BB	6 BC 3 CC	ND

1. Genotypic frequencies in progeny are listed in Table 1. In substrate group 1, the distribution of progeny genotypes is consistent with the uppermost individual in stack A (A4) acting as the sole sire. The immediately adjacent snail, A3, was brooding larvae at the time of collection; had it been the sole or primary sire, the *Mpi-2* A allele would not have been observed in almost half the progeny. However, since 77% of the population was estimated to possess dilocus genotypes *Gpi*(AA, AB, or B)/*Mpi-2* (AA, AB, or BB), the possibility of a contribution by an undetected sire is substantial.

In substrate group 2, the progeny of female Ala were probably sired for the most part by another brooding female (A3), judging from the predominance of the *Gpi* AB genotype (37 of 41 progeny). The predominance of the BB genotype (33 of 36 progeny) at the *Est-2* locus is consistent with this inference, although the parental genotypes are unknown. However, the presence of the *Gpi* BB and BC genotypes, as well as the unexpected occurrence of the *Mpi-2* AB genotype in three individuals, rules out A3 as the sole sire. The *Mpi-2* AB genotype suggests the contribution of a roving male, since it is unlikely that the large brooding female A1b acted as sire. A significant contribution of the only male in the stack, A5, is ruled out by the absence of the *Gpi* α allele in the progeny. This brood is the only one examined that provides unequivocal evidence of multiple paternity, as it contains three different *Gpi* alleles of paternal origin.

The 24 progeny of female A2 in substrate group 3 cannot have been sired solely by either A3 or A4. The presence of the *Gpi* C allele (one individual) is consistent with a

contribution from A3, while the *Mpi-2* A allele (seven individuals) could only have come from A4 (or a visiting male). The limited PGM data also point to A4 as a sire. As 42% of the population was estimated to possess the dilocus genotype *Gpi*(BB or BC)/*Mpi-2*(AA, AB, or BB), an additional sire or sires may have gone undetected.

In substrate group 4, the progeny of female A3 appear to have been sired exclusively by the immediately adjacent individual, A4. All 23 progeny are heterozygotes at the *Gpi* locus, and genotypes at other loci are in accord with this interpretation. The probability of an additional undetected sire is negligible, as we estimate that only 6% of the population possessed genotypes [*Gpi* AA/*Mpi-2* BB/*Pgm*(AA, AC, or CC)] that would have made their contributions undetectable.

The progeny of female A4 (*Gpi* BB) in group 5 may have been sired largely by either individual A6 (*Gpi* BC) or A7 (*Gpi* BB), or both. However, a small contribution by another male (possibly B3) is indicated by the presence of the *Gpi* A allele.

Genotypes found in the progeny of female A1 in substrate group 6 are compatible with the contribution of a single male, A3. We estimate that 44% of individuals in the population possessed genotypes [*Gpi*(AB or BB)/*Mpi-2* BB/*Pgm*(AC, BC, BB, or CC)] that would have made their contributions undetectable.

DISCUSSION

Owing to the small number of polymorphic enzyme loci and the small numbers of progeny scored in this study,

our ability to detect multiple paternity, and conversely to exclude individuals as potential sires, was limited. Nevertheless, these data indicate that (1) typically a single brood is probably sired largely but not exclusively by a single male; (2) sperm can be stored for some time, judging from the apparent male contributions by individuals collected as transitional forms or even as brooding females; and (3) contributions are made by individuals not present in a stack, presumably roving males.

These results extend the direct observations of ORTON (1950) and HOAGLAND (1978), who noted multiple mating within a stack, including copulation between individuals separated by three or four intervening animals. Multiple mating appears to be effective, resulting in genetic contributions from more than one male to single broods. In addition, roving males appear to enjoy some reproductive success. Further study, in the form of detailed field observations coupled with a more powerful form of paternity analysis (*e.g.*, DNA fingerprinting) should greatly improve our understanding of the ecological dynamics of fertilization and paternity in *Crepidula fornicata*, a model system for studies of sex change in the Mollusca.

ACKNOWLEDGMENTS

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The Egg Capsules and Early Life History of the Corallivorous Gastropod *Drupella cornus* (Röding, 1798)

by

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Abstract. The corallivorous muricid gastropod *Drupella cornus* (Röding, 1798) has undergone a marked increase in numbers along the Ningaloo Reef Tract (northwestern Australia) over the last decade. Associated with this population explosion has been a significant increase in the extent of coral predation evident along the reef. The spawning behavior and early life history of *D. cornus* have been studied in the laboratory. Seven *D. cornus* were observed to spawn between 4 and 115 capsules over a period of 1–2 weeks. In the laboratory the distinctively shaped capsules, which averaged $2.8 \times 3.2 \times 1.8$ mm in size, were firmly attached to the aquarium walls. Each capsule contained between 311 and 1384 ($n = 50$) embryos, which hatched, after 20–37 days, into planktonic veligers. No larvae have been successfully reared through to metamorphosis and settlement in the laboratory; however, the size of the protoconch of juvenile *D. cornus* suggests that the veligers may spend extended periods in the plankton.

INTRODUCTION

A number of marine organisms, including species of fish, crustaceans, mollusks, echinoderms and polychaetes, are known to feed, either facultatively or obligately, on scleractinian corals (see ROBERTSON [1970] for a review). Previously, only the asteroid *Acanthaster planci* (crown-of-thorns) has been reported to represent a serious threat to coral reefs (see MORAN [1986] for a review). Over the last 5–10 years, however, the predatory activities of the corallivorous muricid gastropod *Drupella cornus* (Röding, 1798) (see Figure 1) have caused conspicuous and significant damage along the Ningaloo Reef Tract (North-West Cape, Western Australia). STODDART (1989) reported that coral cover in the back-reef zone at Ningaloo has been reduced by more than 75% in two-thirds of the reef.

Drupella cornus is a common and widespread species found throughout the tropical and subtropical shallow waters of the Indo-West Pacific (WILSON & GILLET, 1971). Since the early 1980s, the numbers of *D. cornus* have increased dramatically along the Ningaloo Reef, from an estimated 100–200 snails/km of reef to the present 1–2 million snails/km (STODDART, 1989). AYLING & AYLING (1987) estimated that there are approximately 500 million *D. cornus* in the Ningaloo Marine Park, which encom-

passes an area of 224,000 hectares (MAY *et al.*, 1989). They recorded average *D. cornus* densities of 5.3–18.5/m², and maximum densities as high as 175/m², on the reef flats where *D. cornus* is most abundant; and they calculated a mean feeding rate of 2.6 cm² of *Acropora* plate coral/snail/day, with a range of between 0.6 and 10.1 cm². It has been suggested that coral damage previously ascribed to *A. planci* predation may actually be a result of the activities of *Drupella* (MOYER *et al.*, 1982). The nature of the damage to the coral colonies themselves, and to the reef communities as a whole, is very similar (MOYER *et al.*, 1982; AYLING & AYLING, 1987).

Outbreaks of *Drupella* species have also been reported around islands in southern Japan (MOYER *et al.*, 1982; FUJIOKA & YAMAZATO, 1983), the Philippines (MOYER *et al.*, 1982), and Enewetak Atoll, Marshall Islands (BOUCHER, 1986). MOYER *et al.* (1982) recorded densities of *D. rugosa* as high as 1500/0.5 m² at sites in the Philippines, and they estimated that, between 1979 and 1981, approximately 35% of one of their study reefs in southern Japan, covering an area of approximately 1200 m², was destroyed by *D. fragum* predation.

Little is known about the biology of *Drupella cornus* or the effects that large numbers of this species may have on

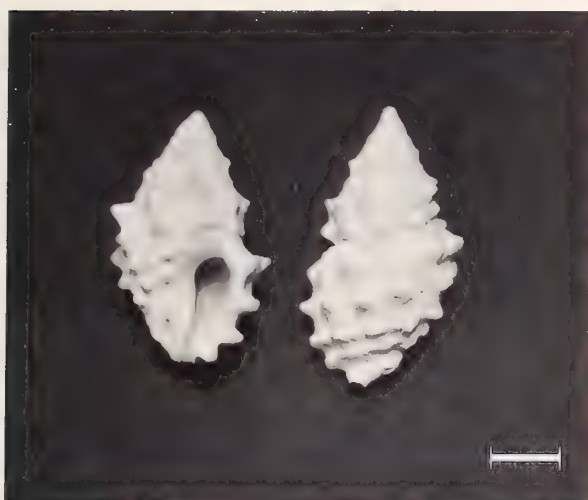


Figure 1

Adult *Drupella cornus* (Röding, 1798) collected from Coral Bay, Ningaloo Reef in February 1990. Scale bar = 1 cm.

coral ecosystems. This paper presents preliminary observations on the early life history of *D. cornus*, with a description of its spawn masses and spawning behavior. Information on the early life cycle of *D. cornus* may be of particular importance in understanding the population outbreaks currently being observed on the Ningaloo Reef.

FIELD SITES

Drupella cornus were collected from shallow-water sites (1–1.5 m depth) at two localities: Coral Bay (14 July 1990 and 17 November 1990) at the southern end of the Ningaloo Reef Tract and Rat Island (12 February 1990 and 16 March 1990) in the Easter Group of the Houtman Abrolhos Islands (Figure 2). The Ningaloo Reef Tract is the largest fringing reef system in Australia, and extends for 280 km along the western side of the North-West Cape peninsula, between Point Murat and Gnarraloo Bay (21°47'S, 114°00'E and 23°38'S, 113°37'E), 1200 km north of Perth, Western Australia. The Houtman Abrolhos Islands are approximately 800 km south of the North-West Cape, and 63 km off Geraldton on the mid-west coast of Australia (between 28°16'S, 113°35'E and 29°S, 114°E). They comprise four groups of islands and reefs (North Island, the Wallabi Group, Easter Group, and Pelsaert Group). More detailed site descriptions and oceanographic information can be found in HEARN *et al.* (1986), SIMPSON & MASINI (1986), AYLING & AYLING (1987), HEARN & PARKER (1988), VERON & MARSH (1988), and MAY *et al.* (1989).

MATERIALS AND METHODS

Groups of 6–30 reproductively mature *Drupella cornus*, ranging in size from 3 to 5 cm shell length, were maintained

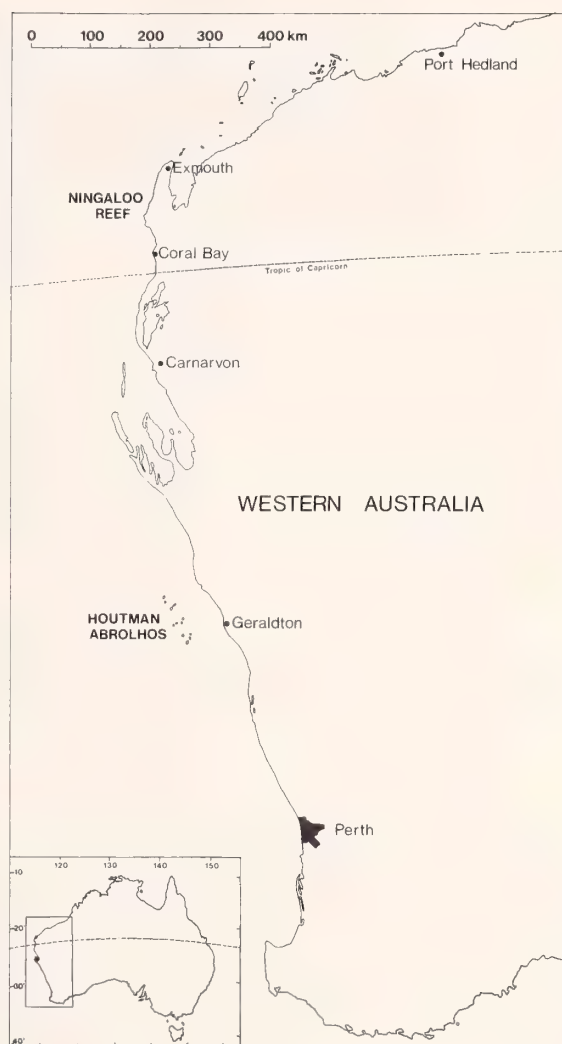


Figure 2

Map showing the field locations mentioned in the text.

in covered 2.5 L plastic aquaria held in the University of Western Australia Marine Biological Laboratory in Perth. Each aquarium was supplied with aeration and running, non-recirculated seawater at 20–26°C, which approximates the temperatures recorded in the natural habitat at the time the snails were collected (see SIMPSON & MASINI, 1986; VERON & MARSH, 1988).

Each aquarium was checked every 2–3 days for the incidence of egg capsules. Egg capsules were left *in situ*, attached to the aquarium walls or floor in running aerated seawater until the final developmental stages were attained, at which point they were transferred into 100-µm filtered seawater. Individual egg capsules were periodically sacrificed and preserved; egg capsule size and the number and size of the developing embryos were recorded. Measurements were made with a Zeiss Technival stereomicroscope and an eyepiece measuring graticule.

Table 1

Summary of the characteristics of the egg capsules produced by *Drupella cornus* under laboratory conditions.

Female ^a	Spawning date (day/month/ year)	Number of capsules	Capsule size ^b (mm)	"Exit pore" size (mm)	Number of eggs/ capsule	Mean egg diameter ^c (μ m)	Vel- igers/ capsule	Mean veliger size ^d (μ m)	Days to early veliger stage ^e	Days to hatch- ing
14	2/IV/90	44	— 3.3 \times 3.3 \times 1.0 —	— 0.5 \times 0.4 —	311 — —	— — —	— 478 392	— — —	11	20–29
3	22–23/VII/90	23	—	—	908	170	—	—	17	
	26/VII/90	6	— — —	— — —	— — —	— — —	564 525 548	— 270 \times 210 260 \times 200	15	27
4	21/VII/90	7	— —	— —	808 —	160 —	— 451	— 280 \times 230	18	27–28
7	24–26/VII/90	33	— 2.9 \times 3.8 \times 2.4 1.8 \times 3.7 \times 2.3	— 0.7 \times 0.45 0.8 \times 0.4	611 — —	180 — —	— 819 610	— — —	16	
9	20–21/VII/90	23	3.5 \times 2.9 \times 1.8 — — — —	0.7 \times 0.5 — — — —	773 — — — —	— — — — —	— 516 384 885 895	— — — — —	19	
	24/VII/90	8	— — — —	— — — —	483 — — —	170 — — —	— 541 528 583	— — — —	17	
	27–28/VII/90	12	3.0 \times 3.2 \times 1.6 3.0 \times 2.6 \times 1.6 2.9 \times 2.8 \times 1.7 2.1 \times 3.1 \times 2.0 1.7 \times 3.2 \times 1.6 2.4 \times 3.8 \times 1.6 3.3 \times 3.2 \times 1.5	0.6 \times 0.5 0.6 \times 0.4 0.5 \times 0.4 0.6 \times 0.4 0.7 \times 0.35 0.7 \times 0.4 0.65 \times 0.5	580 — — — — — —	170 — — — — — —	— 436 497 509 402 491 567	— 260 \times 220 250 \times 210 — — — —	14	
	29/VII/90	14	2.5 \times 3.2 \times 1.8	0.6 \times 0.4	380	180	—	—	21	
	30/VII/90	8	2.2 \times 4.0 \times 2.0 2.9 \times 3.0 \times 1.6	0.7 \times 0.4 0.6 \times 0.5	— —	— —	564 512	— —		
	31/VII/90	8	2.7 \times 3.0 \times 2.0 2.1 \times 3.3 \times 2.4	0.6 \times 0.5 0.6 \times 0.4	484 —	170 —	— 554	— —		
	1/VIII/90	9	3.5 \times 3.2 \times 1.8 3.1 \times 3.1 \times 1.6 3.3 \times 2.8 \times 1.8 3.4 \times 3.3 \times 1.6	0.7 \times 0.5 0.6 \times 0.5 0.7 \times 0.5 0.65 \times 0.5	554 — — —	160 — — —	— 538 544 629	— — — —	18	
	2/VIII/90	12	2.7 \times 3.0 \times 2.1 —	0.8 \times 0.5 —	— —	— —	640 496	— —	21	
	3/VIII/90	10	3.0 \times 2.9 \times 1.6 3.3 \times 2.7 \times 1.7 3.3 \times 3.1 \times 2.0 3.0 \times 2.8 \times 1.8	0.7 \times 0.5 0.7 \times 0.6 0.8 \times 0.5 0.9 \times 0.6	378 — — —	180 — — —	— 516 591 473	— — — —	16	

Table 1
Continued.

Female ^a	Spawning date (day/month/ year)	Number of capsules	Capsule size ^b (mm)	"Exit pore" size (mm)	Number of eggs/ capsule	Mean egg diameter ^c (μ m)	Veli- gers/ capsule	Mean veliger size ^d (μ m)	Days to early veliger stage ^e	Days to hatch- ing
10	4/VIII/90	11	—	—	0 ^f	—	—	—	16	
	29/VII/90	4	—	—	586	160	—	—		
			—	—	—	—	477	—		
			—	—	—	—	701	—		
11	19–20/VII/90	22	—	—	—	—	1384	—	19	28–37
			—	—	—	—	1009	—		
			—	—	—	—	1221	—		

^a Female 14 was collected from the Abrolhos Islands on 16 March 1990; all the other snails were collected at Coral Bay on 14 July 1990.

^b Measurements = height \times length \times width.

^c The mean diameter of eggs that are less than 12 hours old ($n = 20$).

^d Length and depth measurements of recently hatched veliger larvae ($n = 15$).

^e The approximate developmental times, to the late trochophore/early veliger stage, for embryos developing in the laboratory. Mean water temperature for the capsules produced by the Abrolhos Islands snail was 25°C and for those from Coral Bay individuals was 21°C.

^f No eggs were observed in any of the 11 capsules spawned on this date.

Larvae that hatched from the capsules spawned in the laboratory were either reared at 25°C and fed *Dunaliella tertiolecta* or *Isochrysis galbana* (Tahitian strain) at a concentration of 10,000 cells/mL (April 1990) or cultured at 21°C and fed a 1:1:1 mixture of *Isochrysis galbana*, *Chaetoceros gracilis*, and *Pavlova lutheri* at a final concentration of 10,000 cells/mL (July–August 1990). Larvae were tested for metamorphic competence by exposing them to small pieces of live *Acropora* species or coralline-algae-encrusted dead coral. The substratum types selected for initial testing were those suggested from field observations on the distribution of juvenile *Drupella cornus*.

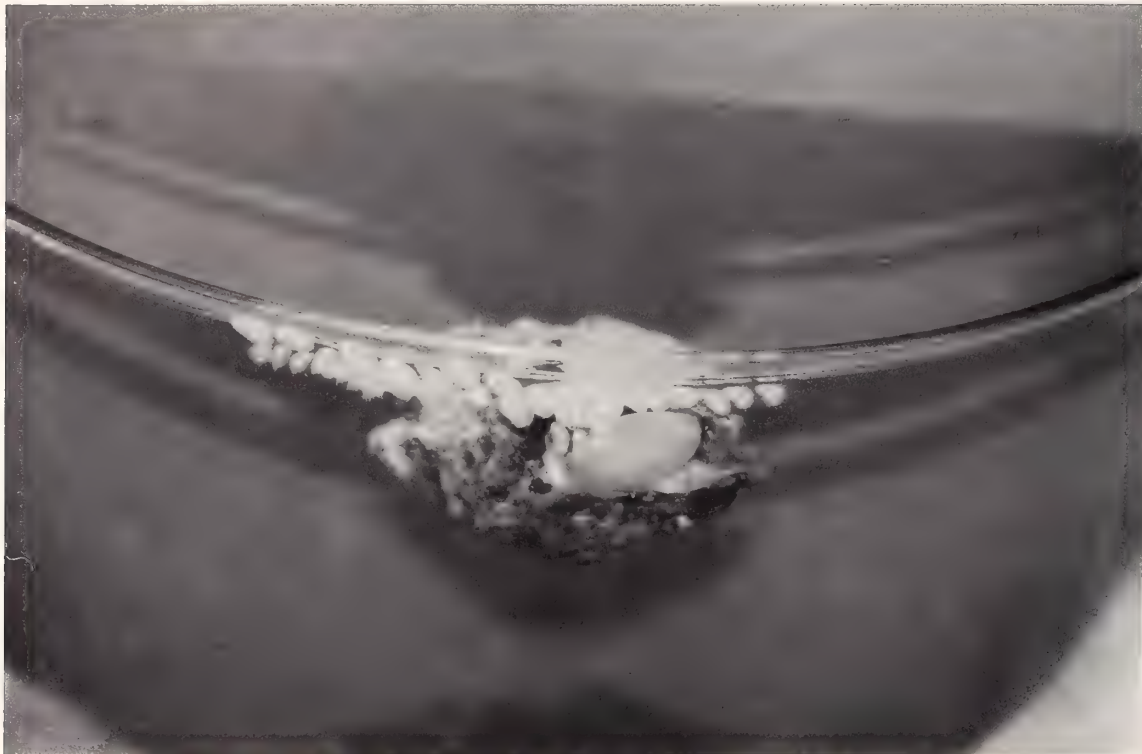
RESULTS

Drupella cornus is gonochoristic, and in the populations at Coral Bay and the Abrolhos Islands, the ratio of the two sexes was approximately 1:1 (NARDI, 1991). Although CERNOHORSKY (1969) listed a number of sexually dimorphic shell characteristics, such criteria are unreliable and the sex of larger living individuals may only be determined with difficulty, by the presence or absence of a penis. Copulation was never observed in the laboratory; however, it appears likely that viable sperm may be retained by the female, since capsule production occurred in the laboratory in isolated females. Spawning generally began within 1–2 weeks of collection, suggesting that the animals that did spawn were either ready to spawn or were already spawning before being brought into the laboratory. Once spawn-

ing had begun it often continued for several days. Under laboratory conditions, spawning has been recorded in April for an Abrolhos Islands individual, and in July for individuals collected at Coral Bay. All the subsequent observations (summarized in Table 1) regarding spawning and embryonic development are based on the egg capsules of the seven individuals that were observed to spawn in the laboratory.

The eggs were deposited in capsules that were attached to the sides or floor of the aquarium (Figure 3), to the plastic mesh lid, or in the overflow pipe. Three of the females (Numbers 3, 7, and 9 in Table 1) were observed to affix capsules (21, 31, and 12, respectively) inside the outlet pipes of their tanks, which are 3-cm lengths of plastic tubing with an internal diameter of 0.5 cm. The majority of the capsules were spawned at night, which is also when *Drupella cornus* is recorded to be most active in the field (FUJIOKA & YAMAZATO, 1983; OXLEY, 1988). The exact length of time it takes for each capsule to be deposited is not known, although preliminary observations indicate that this may take approximately one hour for each capsule. Each female produced a total of 4–115 capsules over a period of 1–16 days. There was no evidence of capsule protection by *D. cornus*, as the females moved away from the spawn mass once spawning had been completed.

The distinctively shaped capsules (Figure 4), which averaged $2.8 \times 3.2 \times 1.8$ mm in size ($n = 25$), were thick-walled and translucent in appearance. Unlike many muricid egg capsules, those produced by *Drupella cornus* were



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not vase-shaped. Each capsule was fixed directly to the substratum by a flattened base, with no evidence of a basal attachment stalk. None was affixed to previously deposited capsules, but each capsule was joined to adjacent capsules by a confluent basal membrane. In cross section the capsules were kidney-shaped, with distinct concave and convex sides, and in general the egg capsules in the same mass were arranged such that the convex side of one capsule was aligned with, and in close proximity to, the concave side of the adjacent capsule. Each capsule had a sealed, oval exit pore (average dimensions = 0.7×0.5 mm, $n = 25$), situated approximately one-third of the way down the concave side of the capsule, through which the veligers left the capsule at hatching.

The capsules from each spawning period were generally deposited in discrete, close-packed, irregular groups. However, one female (Number 9 in Table 1) was observed to undergo extensive movement during some of the spawning events; the capsules produced between 29 July 1990 and 4 August 1990 were attached all over the bottom of the aquarium, often singly or in clusters of 2 or 3 capsules. Occasionally the females were observed to add further capsules to an already established mass during subsequent spawning events. It is difficult to determine if these are atypical spawning behaviors, or whether under natural conditions the females will distribute capsules over a relatively wide area, rather than attaching all the capsules in one location, with several females contributing to each spawn mass.

There was considerable variation between females in the numbers of capsules produced and the numbers of eggs in each capsule. Each capsule contained several hundred embryos, an average of 596 embryos (range = 311–1384) was recorded in the 50 capsules examined. The embryos were distributed around the peripheral areas within the capsules, and were all at approximately the same developmental stage. The eggs were spherical, pale creamy white in color, averaged $170 \mu\text{m}$ in diameter ($n = 200$), and appeared to be embedded within a gel-like substance inside the capsules.

The general patterns of cleavage, gastrulation, and early development of the veligers were essentially the same as described for other indirectly developing prosobranch gastropods (e.g., D'ASARO, 1966; KUMÉ & DAN, 1968). After 2–3 weeks at 21°C , the early veliger stages were evident within the capsules. A small cap-shaped shell developed surrounding the posterior region of the embryo and gradually took on the typical spiral form. Simultaneously, two small velar lobes developed at the anterior part of the body. The visceral mass was packed with yolk, which was largely

absorbed by the time of hatching. The veligers hatched in 27–37 days at 21°C and in 20–29 days at 25°C ; therefore, development time seems to vary with temperature. The newly hatched veligers had dextrally coiled shells with $1\frac{1}{3}$ – $1\frac{1}{2}$ whorls and an average size of $265 \times 215 \mu\text{m}$ (length \times depth) ($n = 75$). The veligers were characterized by the presence of a well-developed bilobed ciliated velum, a foot with operculum, prominent eyespots, and a darkly pigmented anal gland (see D'ASARO, 1966). Characteristic features of the veliger shell included the presence of the larval beak—a prolongation of the outer edge of the shell aperture that extends over the shell opening between the velar lobes—and the distinct grainy appearance of the shell surface (Figure 5). There was a concentration of red/brown pigmentation at the growing edge of the shell in the region of the larval beak and the developing shell columella. Feeding and shell growth appeared to begin soon after hatching. At 21°C , larvae fed on a 1:1:1 mixture of *Isochrysis galbana*, *Chaetoceros gracilis* and *Paolova lutheri* at a final concentration of 10,000 cells/mL grew from an average size of $250 \times 200 \mu\text{m}$ ($n = 11$) to $290 \times 220 \mu\text{m}$ ($n = 16$) within the first 7 days. A distinct demarcation was evident between the shell that grew within the egg capsule before hatching (the protoconch I) and the shell that was grown during the planktonic larval period after hatching (the protoconch II) (see LIMA & LUTZ, 1990).

In the *Drupella cornus* capsules deposited in the laboratory, there was no evidence of significant differences in the number of eggs in the recently spawned capsules and the number of veligers hatching from the capsules at the end of the developmental period (Mann-Whitney *U*-test, $P > 0.05$). Thus, *D. cornus* did not appear to produce food or nurse eggs, and cannibalism did not occur to a significant degree within the capsules spawned in the laboratory.

The morphology of molluscan egg capsules is generally regarded as being species specific. Documentation of capsule characteristics has, therefore, enabled identification of possible *Drupella cornus* capsules in the field. During June–July 1990 and October–November 1990, 14 clusters of capsules (varying between 1 and 41 capsules) very similar in appearance and dimensions to those spawned in the laboratory were found attached within small crevices in the dead bases of *Montipora* and *Acropora* species sampled at Bundegi Reef in the Exmouth Gulf and at Coral Bay. It is not known whether each of the clusters found on the reef was produced by a single female or whether the females tend to be gregarious, depositing their capsules in the same coral crevice, although not necessarily simultaneously. Gregarious behavior during spawning has been observed in a number of muricids (e.g., *Thais haemastoma*

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Figure 3

Abrolhos Islands *Drupella cornus* female spawning in the laboratory (2 April 1990). The 44 capsules were attached, in close proximity to each other, on the side wall of a plastic aquarium. Scale bar = 1 cm.

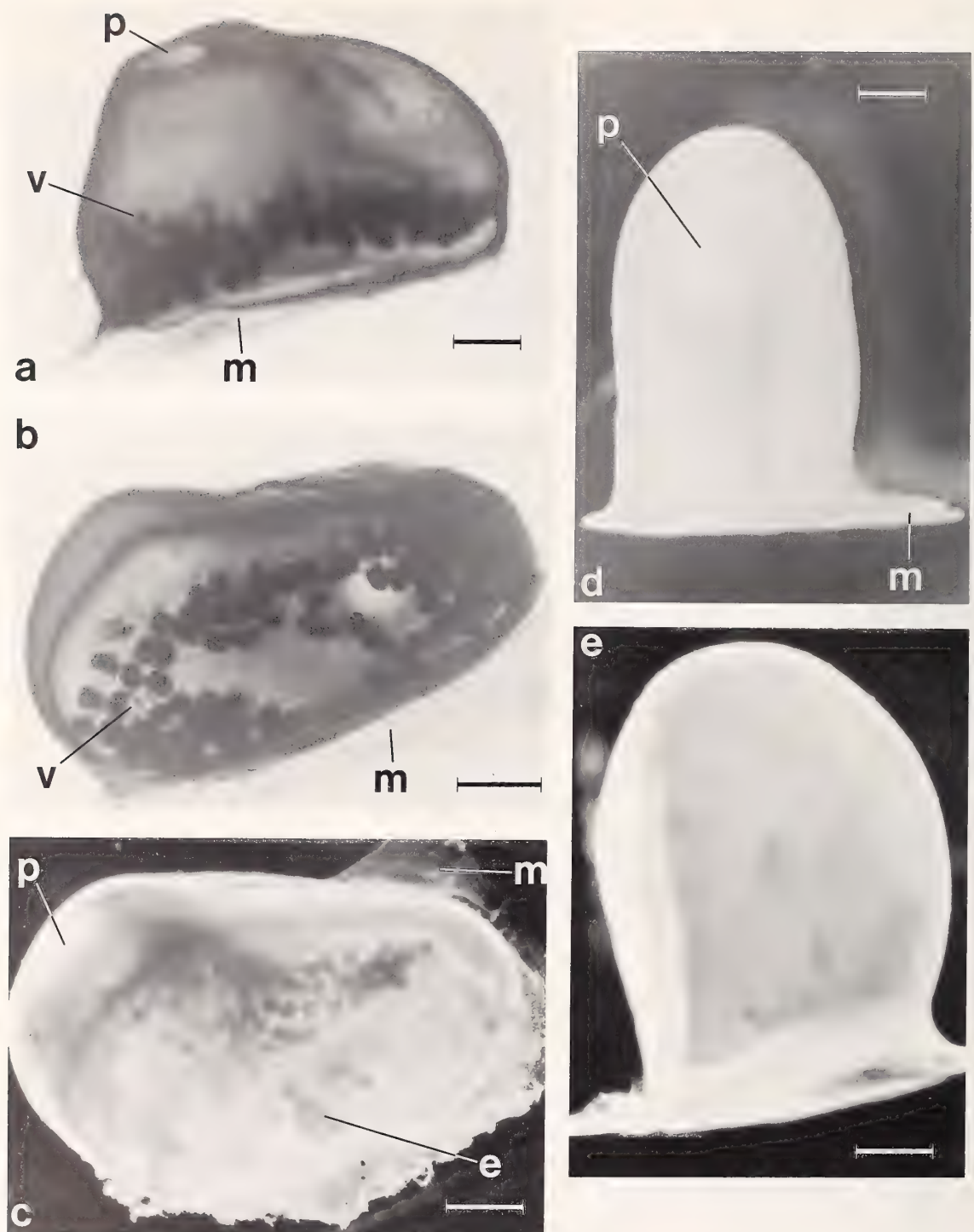


Figure 4

Drupella cornus egg capsules.

a. Side view of an egg capsule containing the early veliger stages of larval development. Scale bar = 0.5 mm.

b. Bottom view of an egg capsule containing the early veliger stages of larval development. Scale bar = 0.5 mm.

c. Bottom view of an egg capsule containing the newly deposited eggs. Scale bar = 0.5 mm.

d. Side view of an egg capsule showing the capsular plug through which the veligers leave the capsule at hatching. Scale bar = 0.5 mm.

e. Side view of an egg capsule. Scale bar = 0.5 mm.

Key: e, embryo; m, basal membrane; p, capsular plug; v, developing veliger.

floridana by D'ASARO, 1966; *Nucella lapillus* by FEARE, 1971; *Ocenebra poulsoni* and *Shaskyus festivus* by FOTHERINGHAM, 1971). The majority of the veligers had hatched from the capsules, but the number in the capsules still containing veligers varied between 284 and 669 ($n = 6$). The capsules deposited in the laboratory contained similar numbers of embryos as the capsules spawned in the field (Mann-Whitney U -test, $P > 0.05$).

DISCUSSION

The presence of a free-swimming planktonic veliger stage in *Drupella cornus* is in contrast to many other species of muricid gastropods that undergo direct development, where the veliger stage is retained within the egg capsule until metamorphosis and miniature adults hatch from the capsules (see SPIGHT, 1975a, 1976). However, many shallow-water tropical species of muricids hatch as long-term (>1 week) veligers, in contrast to species from high-latitude habitats, which metamorphose before hatching (SPIGHT, 1977a). Although planktonic veligers may be produced under the laboratory conditions employed in this study, SPIGHT (1975a, 1977b) cites incidences of different developmental types in geographically separated populations of gastropods, and within single populations either over time, among females, or even among or within broods of a single female. Observations of developing embryos in egg capsules collected in the field indicate that *D. cornus* produces planktonic larvae in the field, at least under some conditions. Furthermore, the embryos of *D. cornus* collected from Okinawa Island, Japan, and maintained in a laboratory also hatched from the capsules as planktonic veligers (AWAKUNI, 1989).

My laboratory observations indicate that the individual fecundity of female *Drupella cornus* may be high; considerable numbers of capsules were deposited by a single female, and each capsule contained several hundred small eggs, all of which appeared to develop into veligers. It is unlikely, however, that fecundity estimates from laboratory observations are truly representative of the potential fecundity of females in the field.

The lifetime fecundity of *Drupella cornus* will be determined by the length of the life of *D. cornus*, the age at which the females start spawning, the frequency of spawning during a female's lifetime, and the interval between successive spawnings, about which no information is currently available. From a comparison of the reproductive and life-history characteristics of a number of muricid gastropods (see SPIGHT *et al.*, 1974; SPIGHT, 1975b, 1979; SPIGHT & EMLEN, 1976), the average adult life-span appears to vary between 1 and 12 years, with sexual maturity being attained after 1–5 years, and the number of clutches being produced per year varying between 1 and 12. Because adult *D. cornus* are relatively large muricids, it may be predicted that they would have a long life expectancy, that they would mature relatively late in life, and that each female would produce one large clutch every year for a

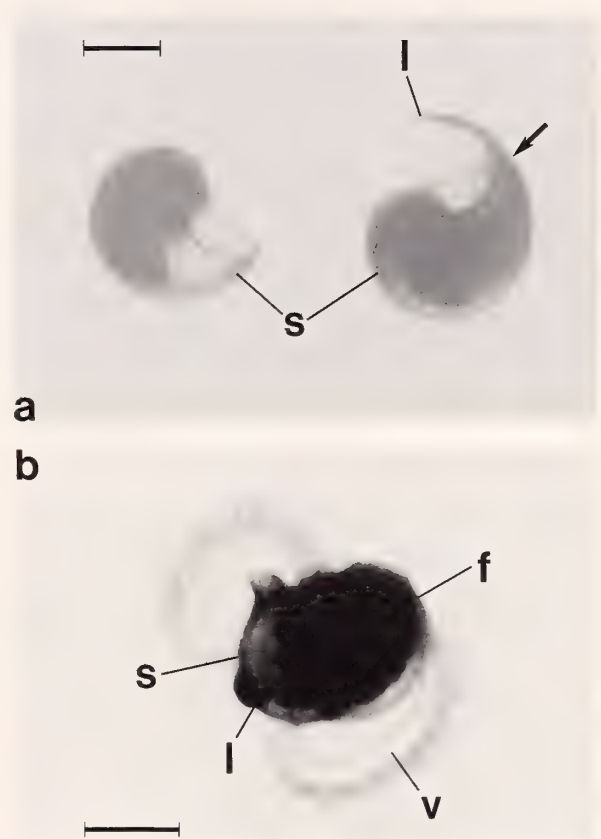


Figure 5

Veliger larvae of *Drupella cornus*.

a. Recently hatched veliger (left side of photograph) and 48-hr-old veliger (ventral view of the shells). Note the prominent larval beak and the demarcation (indicated by the arrow) between the protoconch I and the protoconch II, which marks the point of hatching from the egg capsule. Scale bar = 100 μ m.

b. An 8-day-old veliger fed on *Isochrysis galbana* in unfiltered seawater. Scale bar = 100 μ m.

Key: f, foot; l, larval beak; s, shell; v, velum.

number of successive years. SPIGHT *et al.* (1974) calculated that the lifetime fecundity of *Shaskyus festivus* (an intertidal muricid found on Californian shores and of a similar size to *D. cornus*) was 75,800 embryos, on the basis that each female produced 21 capsules per year, each containing an average of 531 embryos, throughout a reproductive life-span of 6.8 years (FOTHERINGHAM, 1971). This is in contrast to smaller muricids that mature early, have a short life expectancy, and spawn small clutches several times a year, producing relatively few eggs per female lifetime (SPIGHT *et al.*, 1974).

SPIGHT *et al.* (1974) predicted that reproduction is delayed until a snail reaches a size at which it is capable of turning its entire annual net energy intake into eggs. Although no information is available for *Drupella cornus*,

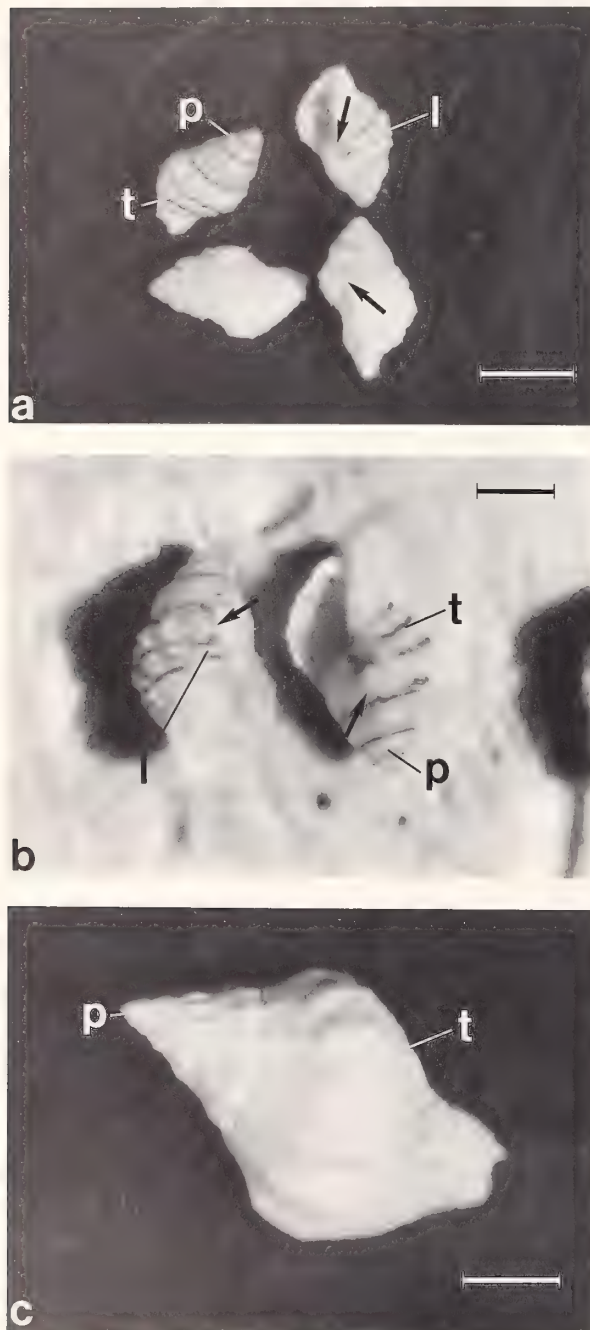


Figure 6

Juvenile *Drupella cornus* collected from the Ningaloo Reef Tract in October–November 1990.

a and b. Shells of juvenile *D. cornus* (1–2 mm total shell length). The arrows indicate the transition in shell growth between the protoconch and teloconch, which occurs at the time of settlement and metamorphosis. Note the fingerlike projection of the larval beak or sinusigera lip on the outer edge of the protoconch shell. Scale bars = 1 mm (a) and 0.5 mm (b).

c. Juvenile *D. cornus*, total shell length 1.07 cm. Scale bar = 0.25 cm.

AWAKUNI (1989) estimated that adults of the related species *D. fraga* would reach their maximum size in approximately 2.5 years. However, the single *D. fraga* veliger that survived through to metamorphosis, 17 days after hatching, was only 275 μm in shell length, considerably smaller in size than *D. cornus* veligers of a similar age (AWAKUNI, 1989). The adults of *D. fraga* are also 1–2 cm smaller than those of *D. cornus*.

The mean egg diameter, veliger hatching size, and developmental periods of *Drupella cornus* are similar to those recorded for other muricid species whose embryos develop without nurse eggs and hatch as veligers (see SPIGHT, 1975a, 1976). Furthermore, the values recorded for *D. cornus* collected at Okinawa Island by AWAKUNI (1989) are very similar—the mean egg diameter was 169 μm , and embryos hatched as veligers, with a mean shell length of 274 μm , after 16–23 days at 24–28°C.

No larvae have so far been successfully reared through to settlement in the laboratory (all died within 2–3 weeks of hatching). However, a relatively extended planktonic life (probably of several weeks) can be inferred because hatching occurs at an early veliger stage when the shell has approximately 1½ whorls and because the protoconchs of juvenile *Drupella cornus* collected in the field were between 3 and 4 whorls in size and between 0.7 and 0.95 mm in length ($n = 47$) (Figure 6). Although his sample sizes were very small, AWAKUNI (1989) found that *D. cornus* veligers reared in the laboratory grew in shell length at a rate of approximately 3.8 $\mu\text{m}/\text{day}$, and reached a shell length of approximately 301 μm in one week and 425 μm after 22 days. The well-defined apertural beak is also characteristic of most long-term planktotrophic prosobranch veligers (D'ASARO, 1966).

Many marine invertebrates exhibit population outbreaks at irregular intervals (COE, 1956), and although population fluctuations may arise because of varying mortality or survival at any of the stages in the life cycle of the organism concerned, it has been suggested that these fluctuations may be primarily attributable to processes affecting the early life-cycle stages. THORSON (1950) found that species with long planktonic larval lives (2 weeks to 3 months) are the most likely to undergo large fluctuations in numbers from year to year because of the vagaries of a planktonic existence, while species with relatively constant populations have either very short planktonic stages (hours or days) in their life cycles or undergo direct development. It is likely, therefore, that an understanding of the early life history of *Drupella cornus* will contribute towards an explanation for the recent increase in the numbers of the snail along the Ningaloo Reef. Further research into the early life history of *D. cornus* will need to concentrate on determining the length of the larval life, the identity of larval predators (both pelagic and benthic), and the selectivity of the larvae towards different substratum types.



Key: l, larval beak; p, protoconch; t, teloconch.

ACKNOWLEDGMENTS

This project is funded by the Australian National Parks and Wildlife Service States Cooperative Assistance Program (Project No. 4465), for which I am grateful. I would also like to thank the University of Western Australia and the Western Australian Fisheries Department for allowing me to use their laboratory facilities. I am especially grateful for all the assistance received from the staff of the Department of Conservation and Land Management at Woodvale and at Exmouth. The advice of Mr. M. Williams with respect to the statistical analysis is also gratefully acknowledged. Special thanks to Mr. T. Cooper, Mr. P. Harding, Mr. S. Lemmens, Ms. S. Mercer, Mr. A. Rockall, Mr. C. Scott, Ms. E. Stroud, Ms. M. Thornton, and Mr. A. Williams for their unfailing help in the field; and to Dr. J. Stoddart, Mr. K. Nardi, and Mr. B. Marinovic for their helpful advice and discussions. Drs. R. Black, T. Friend, T. Start, and J. Stoddart and two anonymous referees read and commented on the preliminary drafts of this manuscript.

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Mantle-Mediated Shell Decollation Increases Posterior Aperture Size in *Dentalium rectius* (Scaphopoda: Dentaliida)

by

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Abstract. In Scaphopoda, incurrent and excurrent water flow through the mantle cavity occurs primarily via the posterior aperture, located at the apex of a tusk-shaped shell. However, maintenance of a sufficiently large posterior opening to the exterior is not accommodated by normal anteriorly directed shell growth, which progressively diminishes the posterior aperture relative to body size. A supplementary increase in posterior aperture size correlated with growth of the organism is therefore necessary to facilitate the passage of respiratory currents, gametes, and waste materials from the mantle cavity. Shell morphometrics, ultrastructure, and direct observations of live specimens of *Dentalium rectius* confirm that such an increase does take place, and is due primarily to decollation of the shell through dissolution by the posterior mantle. While an increase in posterior aperture size by shell dissolution and truncation had been previously predicted, shell decollation has not been previously recorded from the class. The removal of an apical portion of shell, as opposed to dissolution of the aperture rim, is necessitated in *D. rectius* and some other Dentaliida by the secretion of a secondary shell by the posterior mantle margin.

INTRODUCTION

The shell of *Dentalium rectius* Carpenter, 1865, is typical of the Dentaliida, being a slightly curved, translucent cone reaching 7 cm in length. As with all members of the class Scaphopoda it is open at both ends, with extension of the burrowing foot and the feeding captacula through the anterior aperture (Figure 1) and passage of both inhalant and exhalant respiratory currents through the posterior opening (YONGE, 1937). While the major portion of the scaphopod shell is secreted by the anterior mantle margin (and referred to here as the primary shell), a thin, secondary tube of shell that is produced by the posterior mantle margin often extends from the apex of the primary shell (Figure 1). Such a secondary shell is found only among several dentaliid scaphopod genera (STASEK & McWILLIAMS, 1973; PALMER, 1974). Shell secretion correlated with soft-tissue growth proceeds anteriorly, by a widening of the anterior aperture accompanied by a slight

spiral along the shell length, producing the characteristic tusklike shape.

The consequences of this shell growth pattern to certain physiological requirements have been noted by LACAZE-DUTHIERS (1856), PILSBRY & SHARP (1897), and FISCHER-PIETTE & FRANC (1969). With increasing size of the animal, a constant posterior aperture size would become progressively smaller in relation to body size, and eventually be inadequate for the passage of respiratory currents, the release of gametes, and the elimination of feces. While the apical larval shell is lost at an early stage (LACAZE-DUTHIERS, 1856), a continual increase in posterior aperture size with growth of the animal has been predicted to occur to ensure the maintenance of adequate exchange with the external environment (LACAZE-DUTHIERS, 1856; PILSBRY & SHARP, 1897; FISCHER-PIETTE & FRANC, 1969).

FISCHER-PIETTE & FRANC (1969) and STASEK & McWILLIAMS (1973) suggest that, in addition to its role in secondary shell secretion, the posterior mantle margin of scaphopods may increase posterior aperture size by dissolution or reabsorptive truncation of the shell apex. Laboratory observation of shell decollation (the loss of the

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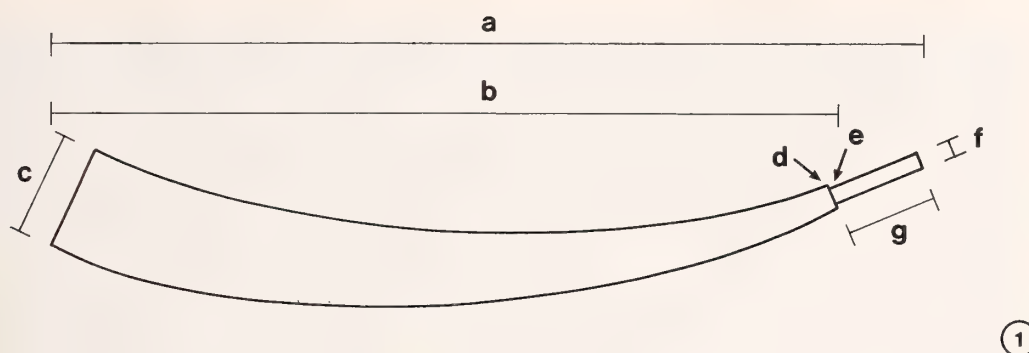


Figure 1

Schematic diagram showing measurements taken on all shells. Dorsal is to the top, anterior to the left. Key: a, total length; b, primary shell length; c, anterior aperture height; d, primary shell apex height; e, secondary shell base height; f, secondary shell apex height; g, secondary shell length. Measurements of height represent diameter along the dorsoventral axis.

posterior or apical portion of the shell) in *Dentalium rectius* prompted an investigation of the posterior shell growth pattern and an examination of discarded and intact shell apices for evidence of the shell loss mechanism.

MATERIALS AND METHODS

Live *Dentalium rectius* for observation were dredged from Imperial Eagle Channel, Barkley Sound (48°52.7'N, 125°11.1'W) near Bamfield, British Columbia, in June 1985, while shell morphometrics were performed on specimens collected from Satellite Channel (48°42.6'N, 123°31.9'W) near Victoria, British Columbia, from October 1987 to February 1988. Voucher specimens have been deposited at the California Academy of Sciences (San Francisco), catalogue No. 075615.

Scaphopods were maintained at Bamfield Marine Station, British Columbia, over a four-day period in sediment (10–13 cm deep) from the biotope sieved to ≤ 1 mm. The sediment and scaphopods (70 specimens in total) were held in plastic beakers of two sizes: 800 mL (10-cm diameter, 2 individuals per beaker, 15 sets) and 1.5L (15-cm diameter, 10 and 20 individuals per beaker, 2 and 1 sets respectively). To maintain aeration of sediment, beakers with doubled 1-mm-mesh sides were used and placed in running seawater ($10 \pm 0.5^\circ\text{C}$). The apical shell of $>80\%$ of the specimens (at least 57/70) was seen level with or above the sediment surface at least once, when examined at 1–12 hr intervals. Shell decollation was observed in one of the scaphopods; the discarded shell apex was later fractured and examined by scanning electron microscopy (SEM).

Shell measurements (Figure 1) were made at $10\times$ magnification using a Zeiss dissecting microscope and ocular micrometer. The primary shells of 23% of the specimens were broken during the sampling process and were excluded from subsequent analyses of shell characters; shells with repaired breakages were not excluded. Character re-

lationships were described by linear regression using least mean squares (ZAR, 1984). Of the measurements taken, anterior aperture height best represented growth (soft-tissue dry weight) as described by the allometric relationship: $\log(y) = 0.238 \log(x) + 0.197$, $r^2 = 0.94$, $P < 0.0001$, $n = 43$ (Figure 2). The absence or presence and the position of a shallow notch at the apex of the primary shell (Figure 3) were noted in a sample of 131 scaphopods (Table 1). These specimens spanned the entire sampled size range (as shown in Figure 2); 93.6% could be sexed by the external appearance of gonads through the semi-transparent shell, whereas the remainder were among the smallest specimens and appeared to be juveniles. The rates of decrease in the size of the posterior aperture per unit length, or taper, of the primary and secondary shells were calculated as follows:

Table 1

Summary of primary shell morphological characteristics in *Dentalium rectius*.

	With secondary shell	Without secondary shell	Totals
All specimens			
Notched	102	11	113 (86.3%)
Not notched	1	3	4 (3.0%)
Repaired breakage	14	—	14 (10.7%)
Totals	117 (89.3%)	14 (10.7%)	131 (100.0%)
Notched shells			
Ventral notch	98	9	107 (94.7%)
Dorsal notch	3	1	4 (3.5%)
Both	1	1	2 (1.8%)
Totals	102 (90.3%)	11 (9.7%)	113 (100.0%)

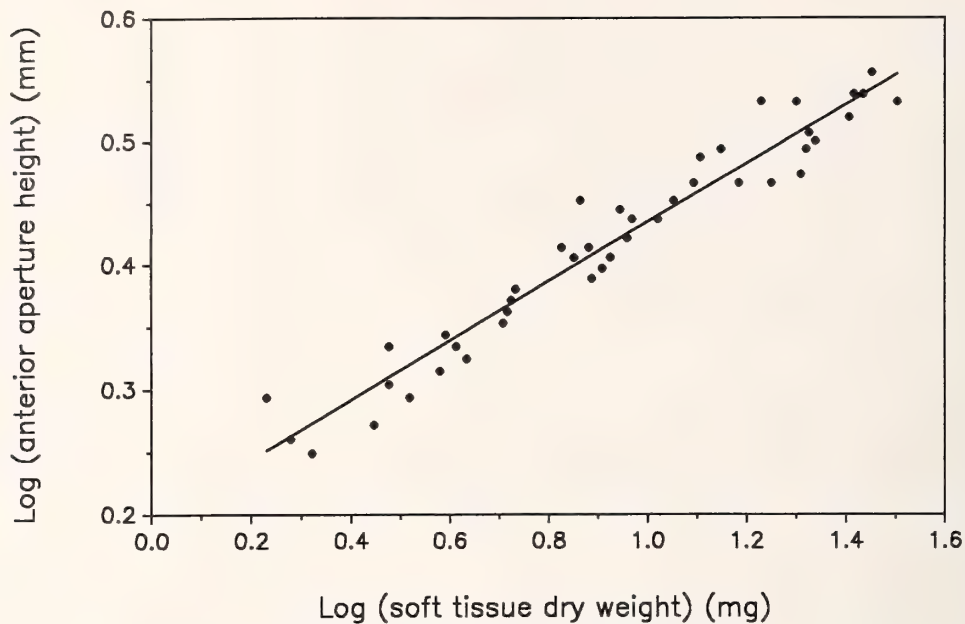


Figure 2

Plot of log (anterior aperture height) against log (soft tissue dry weight). $\log(y) = 0.238 \log(x) + 0.197$, $r^2 = 0.94$, $P < 0.0001$, $n = 43$.

Primary shell taper

$$= \frac{\text{primary shell base (anterior aperture)} - \text{primary shell apex}}{\text{primary shell length}}$$

Secondary shell taper

$$= \frac{\text{secondary shell base} - \text{secondary shell apex (posterior aperture)}}{\text{secondary shell length}}$$

The means of primary and secondary shell taper were compared using the Student *t*-test (ZAR, 1984).

Shells examined by SEM were rinsed with double-distilled water, dried at room temperature, mounted on aluminium stubs, and, in some cases, fractured using a fine stainless-steel probe. Specimens were gold coated prior to viewing in a JEOL JSM-35 scanning electron microscope.

RESULTS

Apical Shell Morphology

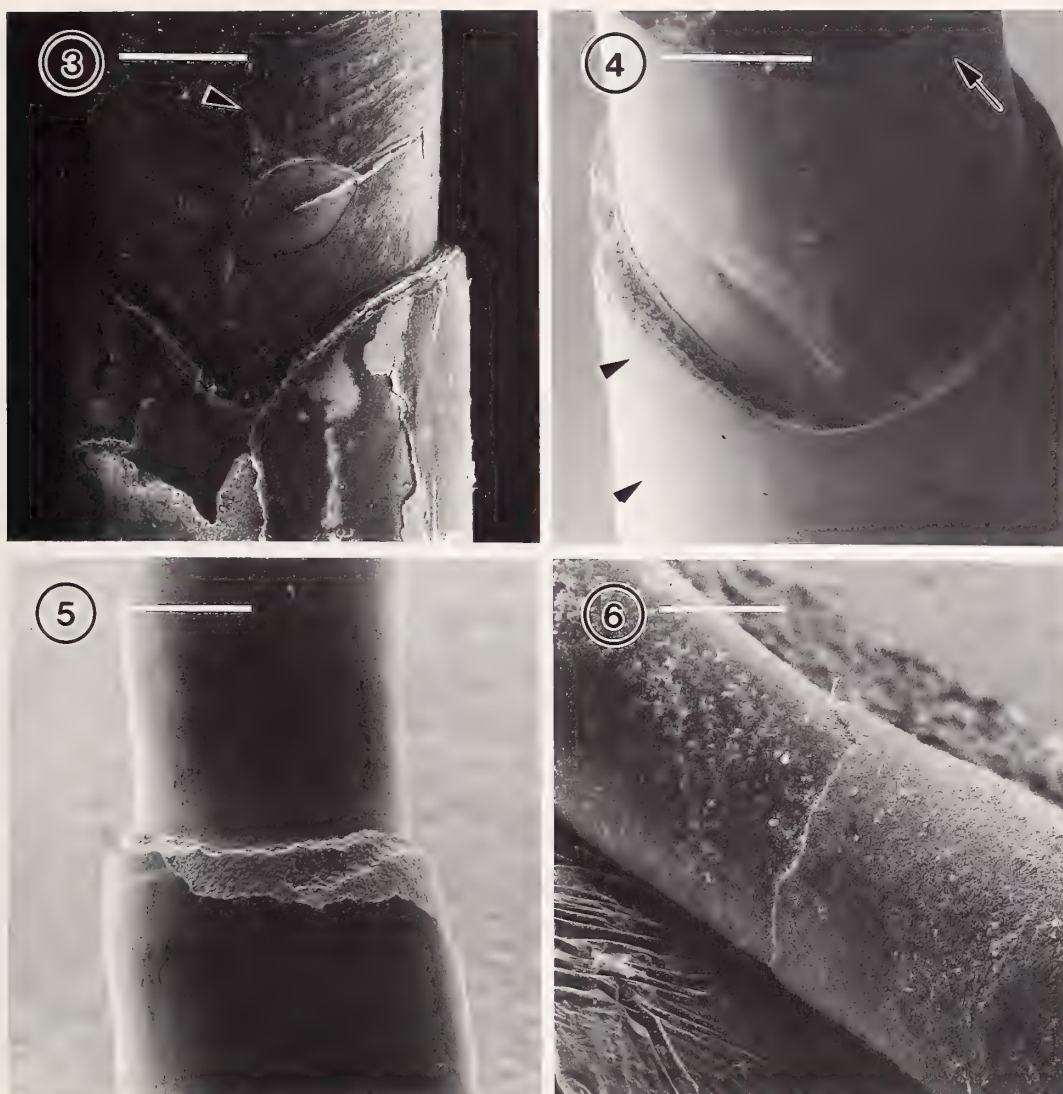
Observations on apical shell morphology are presented in Table 1. The primary shell apex of most shells (86.3%) bears a notch (Figures 3, 4), which is usually found on the ventral (convex) side (94.7%). Otherwise, specimens have a jagged primary shell apex indicating a repaired break (10.7%) (Figures 5, 6) or a smooth apex with no notch (3%). The primary shell is secreted by the anterior mantle margin, which is reflected by the presence of cir-

cular growth lines (Figures 5, 6), although these are often not apparent at the apex of the primary shell owing to erosion (Figures 3, 4).

A secondary shell was present in 89.3% of the specimens (Table 1). The secondary shell is secreted by the posterior mantle margin, which produces V-shaped growth increments and a ventral suture line (Figures 3, 4). The apex of the secondary shell was usually broken, although a notch was noted at the apex on intact shells. Secondary shell growth was discontinuous in 13 cases (7.6% of all specimens with a secondary shell); nine of these had a notched primary shell with a subsequent break in the secondary shell having been repaired (one with two breaks), three had a notched primary shell with a notched disruption in the secondary shell, and one had a break repaired in the primary shell apex with a notched disruption in the secondary shell.

Observation of Shell Decollation and Evidence of Shell Dissolution

During observations of live *Dentalium rectius*, shell decollation was observed in a specimen approximately 3 cm in length (about 26.7 mm primary shell, 3.3 mm secondary shell), with the posterior shell protruding 7–9 mm from the sediment. The shell apex had detached and fallen over, and was found resting at an angle between the sediment surface and the new aperture rim. The scaphopod had not changed position appreciably over the previous hour. When the container was disturbed several minutes later, the



Explanation of Figures 3 to 6

Figures 3–6. Junction of primary (lower) and secondary (upper) shells.

Figure 3. Ventral view of notched primary-secondary shell junction. Note the V-shaped notch at the primary shell apex, the V-shaped growth lines and median suture line (arrowhead) of the secondary shell, and the eroded primary shell. Scale = 0.3 mm.

Figure 4. Ventral view of notched primary-secondary shell junction. Note the circular growth lines of the primary shell (arrowheads and lower left corner), V-shaped notch at the primary shell apex, and the V-shaped growth lines, median suture line, and simple prismatic structure (arrow) of the secondary shell. Scale = 0.2 mm.

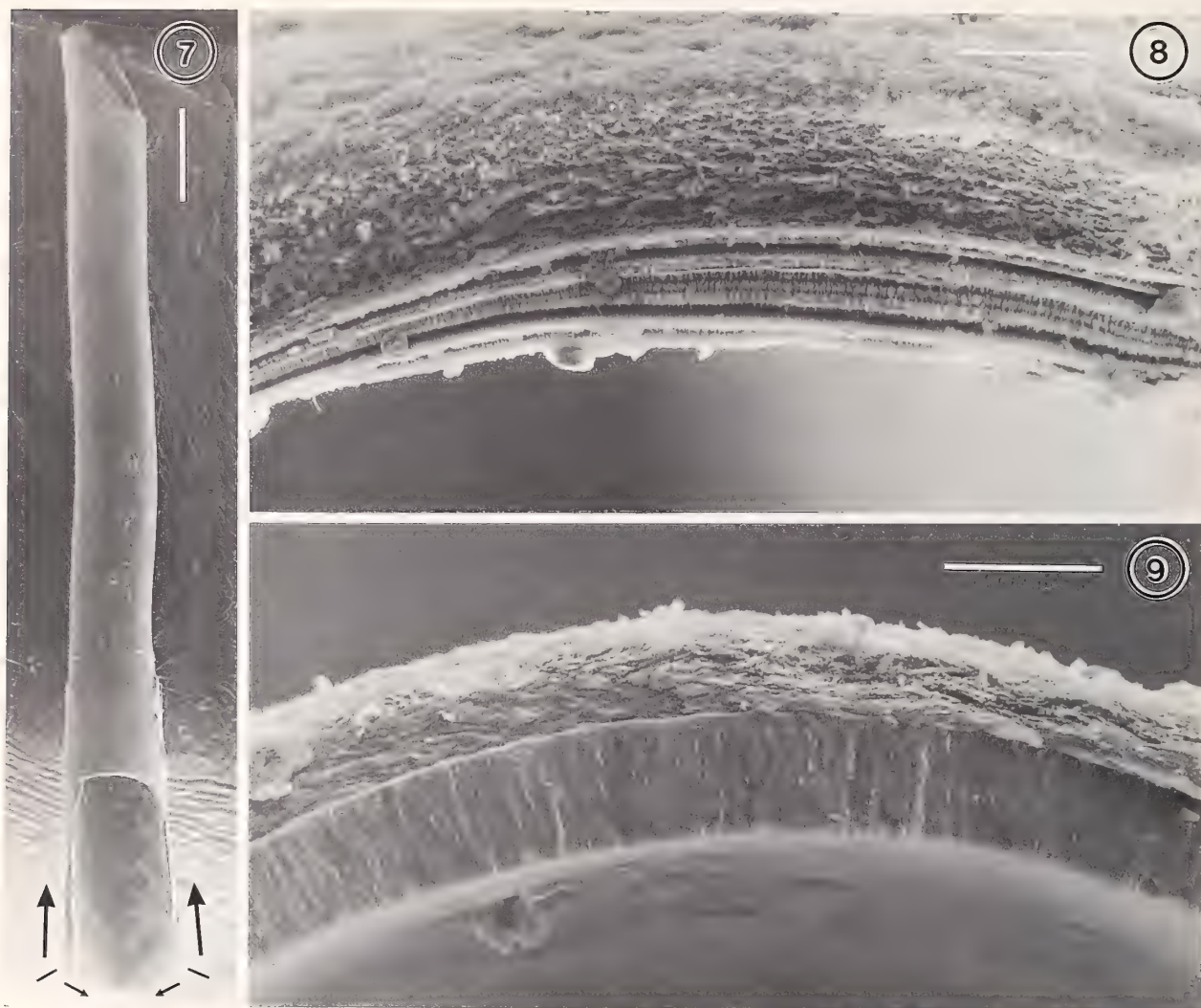
Figure 5. Lateral view of primary-secondary shell junction that lacks a notch (ventral to the right). Note the circular growth lines and jagged apex of the primary shell. Scale = 0.2 mm.

Figure 6. Dorsal view of primary-secondary shell junction that lacks a notch. Note the jagged apex of the primary shell. Scale = 0.2 mm.

scaphopod burrowed deeper into the sediment, leaving the detached portion of shell on the sediment surface. The animal appeared healthy (*i.e.*, vigorous burrowing movements by the foot) when examined two days later.

The discarded shell apex measured 5.15 mm in length,

of which approximately 1.84 mm was primary shell possessing a jagged apex (Figures 6, 7). At the point of separation the height of the detached shell was 0.67 mm, tapering to 0.38 mm posteriorly (Figure 7). The posterior aperture of the scaphopod therefore increased by 0.29 mm,



Explanation of Figures 7 to 9

Figure 7. Dorsal view of discarded shell apex, with lower dorsal portion removed (fracture line indicated by large arrows). Note the V-shaped line of decollation from the primary shell (small arrows). Scale = 0.5 mm.

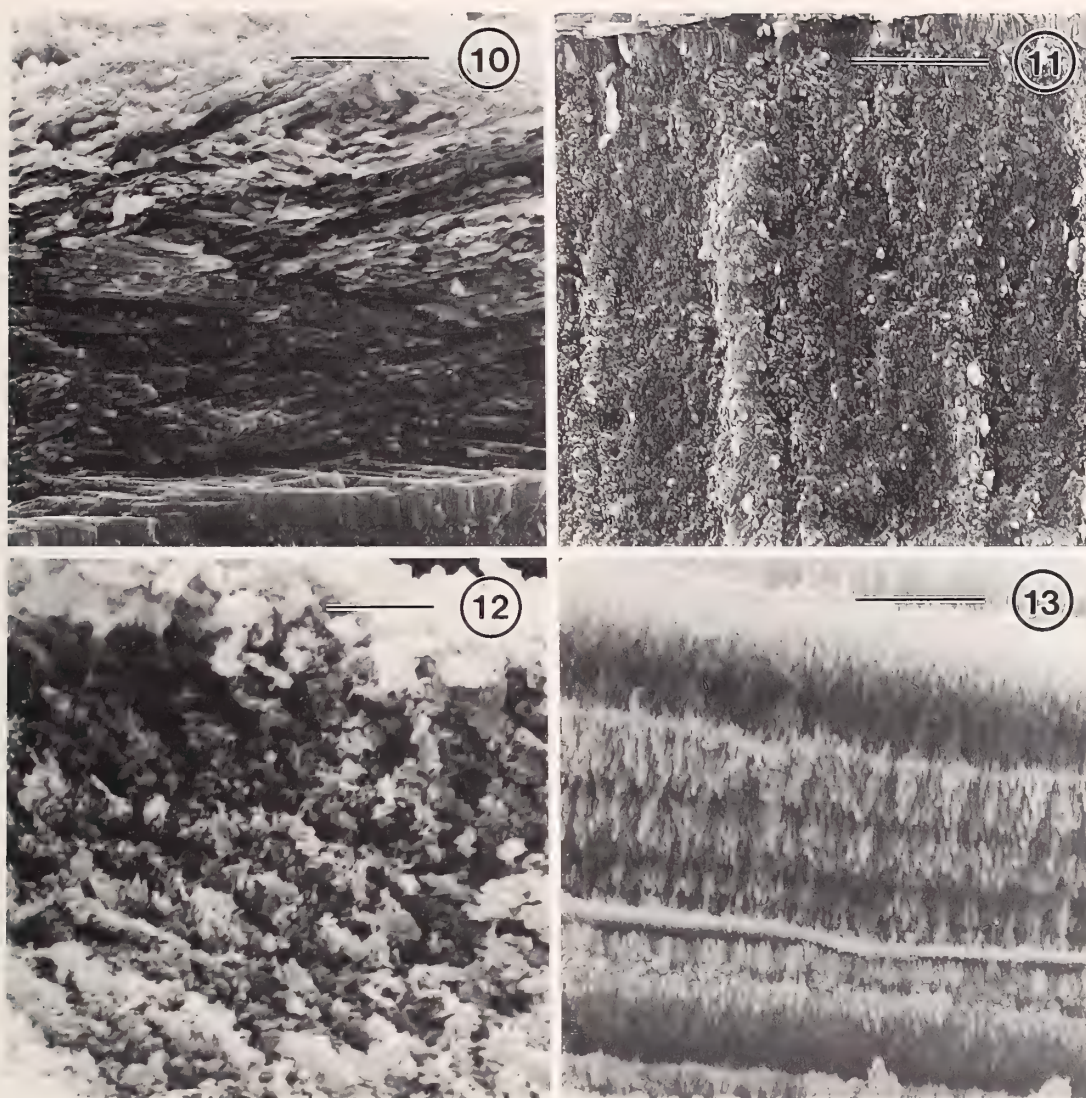
Figure 8. Etched shell layers where decollation from the primary shell occurred. Note the deeply eroded appearance of the two distinct shell layers. Scale = 30 μ m.

Figure 9. Fractured edge of same shell. In the same orientation as in Figure 8 (cross section). Note the clearly defined shell microstructure. Scale = 30 μ m.

or $1.8\times$ the original diameter. The edge of the discarded shell, where separation from the primary shell occurred, clearly showed evidence of dissolution by the loss of mineralized material from the shell layers (Figure 8) when compared to a fractured edge of the same discarded shell (Figure 9). The anterior fractured edge of the discarded shell shows the two layers of aragonitic calcium carbonate of the primary shell, an outer crossed lamellar layer (Figure 10) and an inner simple prismatic layer (Figure 11) that is continuous with the single, prismatic layer of the secondary shell (Figure 4). Comparison with the corre-

sponding shell layers at the edge of detachment from the scaphopod (Figures 12, 13) shows a strong etching or erosion; there is a loss of the crossed lamellar crystal arrangement accompanied by the production of a rough, irregular surface with deep interstices (Figure 12), whereas the uneven but solid face of the fractured prismatic layer in Figure 11 contrasts with the deeply eroded prismatic layer where detachment occurred, producing layered cavities and rounded remains of the crystal structure (Figure 13).

The internal surface of the discarded shell apex revealed



Explanation of Figures 10 to 13

Figure 10. Outer crossed lamellar layer of the decollated shell, fractured region. Scale = 5 μm .

Figure 11. Inner simple prismatic layer of the decollated shell, fractured region. Scale = 5 μm .

Figure 12. Outer crossed lamellar layer of the decollated shell at site of decollation, showing evidence of dissolution. Same orientation as in Figure 10. Scale = 5 μm .

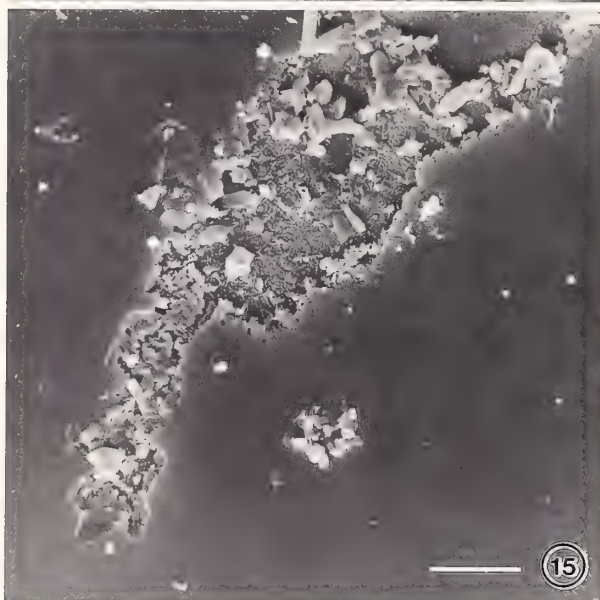
Figure 13. Inner simple prismatic layer of the decollated shell at site of decollation, showing evidence of dissolution. Same orientation as in Figure 11. Scale = 5 μm .

partial shell dissolution at a number of locations posterior to the site of detachment (Figures 14, 15), and stereoscopic SEM observations confirmed these markings to be depressions into the shell. Close examination revealed a rough surface which differed substantially from the normally smooth, slightly undulating topography of the internal shell (Figure 15). The V-shaped, ventral orientation of these scars corresponded in form and position to the edge where separation of the shell eventually occurred (Figure 14),

and with the notches normally found at the primary shell apex. SEM examination of the internal shell surface of several specimens revealed no other markings posterior to the point of retractor muscle insertion.

Analysis of Shell Measurements

Analysis of shell characters shows that decollation (indicated by a notch on the primary shell apex) produces

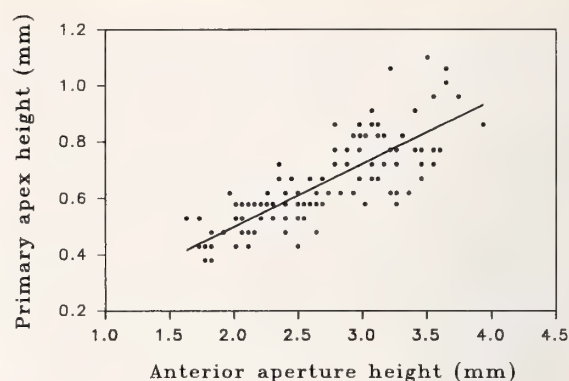


Explanation of Figures 14 and 15

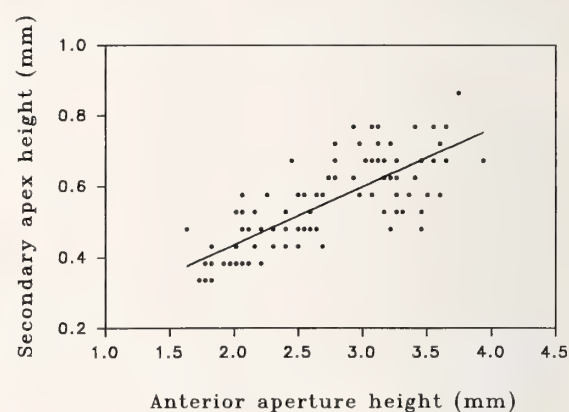
Figure 14. Discarded shell, view of internal ventral surface. Note three sets of V-shaped scars (arrowheads). Double arrowhead, detachment edge. Scale = 0.1 mm.

Figure 15. Scar on internal ventral surface of detached shell, produced by shell dissolution. Scale = 20 μ m.

increased posterior aperture sizes (represented at the time of decollation by notched primary shell apex height) with growth (Figure 16). While subsequent secondary shell growth originates from the internal surface of the primary shell apex (Figures 3–6), it does not taper as much as the primary shell (Table 2) and so the increased aperture size is conserved (Figure 17).



16



17

Explanation of Figures 16 and 17

Figure 16. Plot of anterior aperture height against primary apex height for notched shells (shells which have been decollated), with or without a secondary shell. $y = 0.22x + 0.05$, $r^2 = 0.63$, $n = 110$.

Figure 17. Plot of anterior aperture height against secondary apex height, notched shells. $y = 0.16x + 0.11$, $r^2 = 0.51$, $n = 100$.

DISCUSSION

In order to maintain sufficient exchange between the external environment and mantle cavity throughout scaphopod ontogeny, a secondary modification of shell shape that increases posterior aperture size with growth of the animal must take place. Such an increase occurs in *Dentalium rectius*, thereby accommodating greater respiratory currents circulating through a larger mantle cavity and facilitating the passage of increasing fecal material and gametes. The removal of shell material to achieve this could occur in a number of ways, such as by abrasion by sediments while burrowing or the gradual dissolution of the aperture rim by the mantle. However, the secretion of a secondary shell by the posterior mantle in *D. rectius* precludes continual dissolution or erosion of the primary shell rim as a mechanism for increasing posterior aperture di-

Table 2

Comparison of primary and secondary shell taper in *Dentalium rectius*, for shells that have been decollated (have a notch on the primary shell apex; $n = 102$). The negative minimum value indicates a secondary shell that increased in width with length.

Taper rate (mm/mm)	Primary shell	Secondary shell
Mean \pm SE*	0.053 \pm 0.001	0.01 \pm 0.006
Minimum	0.037	-0.056
Maximum	0.086	0.500

* t -test: $0.001 < P (|t| \geq 7.289) < 0.0001$.

ameter. Instead, the entire secondary shell and a posterior portion of the primary shell must be removed. While hap-hazard and potentially fatal to the scaphopod, extrinsic breakage of the primary shell apex, with subsequent repair by secondary shell growth, may increase posterior aperture size in a small percentage of the sampled population at any one time (e.g., 10.69%, Table 1). Shell decollation, by dissolution of the shell anterior to the primary shell apex resulting in the detachment of an apical portion of the shell, is a more effective mechanism for increasing aperture size with growth of the animal. As observed under laboratory conditions, *D. rectius* can decollate the posterior portion of its shell in this way. Repeated periodically, this would account for the observed increase in posterior aperture size in this species, and the presence of a ventral notch in the primary shell apex of almost 90% of the study population across the entire sampled size range (Figure 18). The V-shaped internal scars and detachment edge of the discarded shell, producing a notch in the new primary shell apex similar to that found in most specimens, resemble surfaces subjected to shell dissolution (DEITH, 1985; SIGNOR, 1985). The consistent orientation, shape, and size of the scars suggest that removal of shell material resulted from secretions of a discrete band of the underlying mantle, in contrast with the large area of outer pavilion epithelium thought to be involved in secondary shell secretion (STASEK & MCWILLIAMS, 1973). It is not possible, however, to specify the precise mechanism of shell removal beyond invoking some type of dissolution or chemical erosion of calcium carbonate; shell reabsorption would require active uptake by the mantle of shell materials, as noted by SIGNOR (1985). FISCHER-PIETTE & FRANC (1969) point out that the process by which scaphopods enlarge the shell anteriorly while progressively shortening it at the posterior end results in the gradual loss of the complete juvenile shell, and the progressive loss of the older portions of the adult shell. This necessitates an anterior shift in the point of retractor muscle insertion as growth proceeds. While no SEM evidence for this was found in the shells examined, it is likely that any scars resulting from such a shift would be obscured by shell secretion of the underlying mantle.

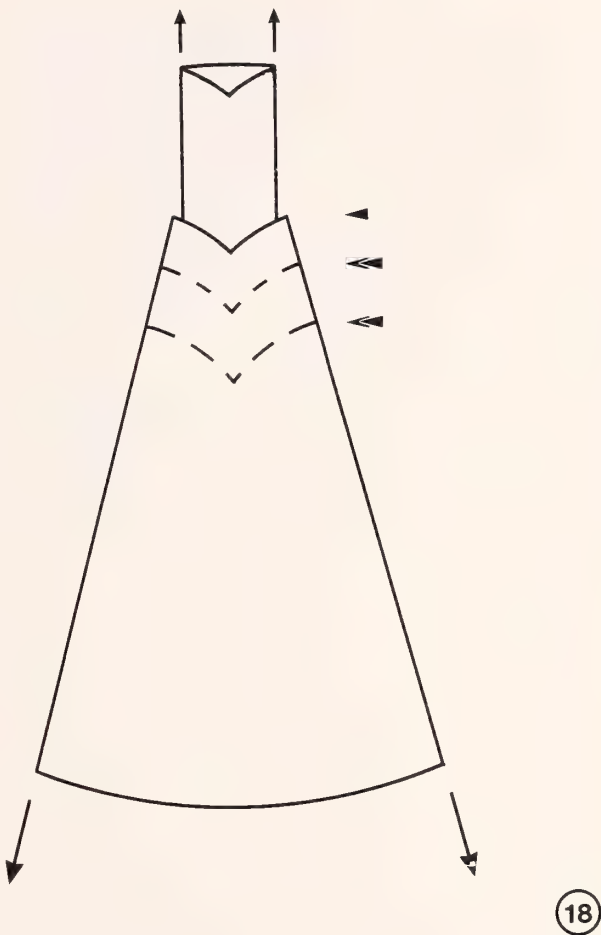


Figure 18

Schematic diagram of shell growth and model for posterior aperture enlargement through decollation of the primary shell. The shell is viewed from the ventral side, showing notches in primary and secondary shells. Most recent (arrowhead) and possible future (double arrowheads) sites of shell decollation are indicated (large arrows, direction of primary shell growth; small arrows, direction of secondary shell growth).

These results indicate that the distinctive primary and secondary shell morphology found in *Dentalium rectius* is not simply due to shell repair following breakages or predation by the ratfish *Hydrolagus colliei* as previously suggested (SHIMEK, 1989), although this may account for some proportion of the approximately 10% of the sampled population with repaired primary shell apex breakages. Instead, secondary shell secretion appears to be a normal program of shell growth following mantle-mediated shell decollation. The function of the secondary shell in *D. rectius* and some other dentaliids (e.g., *Episiphon*) is open to speculation; perhaps it affords protection to the sensory epithelia of the posterior mantle edge or pavilion (REYNOLDS, in press) while maximizing posterior aperture increase. It

is also important to note that while the original description of *D. rectius* (Carpenter, 1864, in PALMER, 1958; CARPENTER, 1865) makes no mention of the sculpture of the posterior aperture, the description of the subgenus *Rhabdus* by PILSBRY & SHARP (1897), which identifies *D. rectius* Carpenter, 1865, as the type species, states that a notch, slit, and secondary shell are absent. EMERSON (1962), however, found that the posterior aperture in *Rhabdus* occasionally has the inner shell layer extended as a thin tube. *Rhabdus* has since been elevated to full generic status by PALMER (1974). Apical shell morphology has been an important shell character in scaphopod taxonomy (e.g., EMERSON, 1962; PALMER, 1974) although the reliability of this and other shell characters has been questioned (SHIMEK, 1989). In all respects, the study populations fit the original description of *D. rectius* and those of recent accounts of northeastern Pacific scaphopods, which also refer this species to the genus *Dentalium* (KOZLOFF, 1987; SHIMEK, 1989). Therefore, it would seem prudent in this report to continue to use the genus-taxon *Dentalium* pending taxonomic review or redescription of *Rhabdus*.

Decollation in *Dentalium rectius* results in loss of the secondary shell and usually the oldest portion of the primary shell, the production of a notch in the shell apex prior to secondary shell regrowth, and an increase in posterior aperture size. Decollation is likely repeated periodically during growth and is an important physiological mechanism for maintaining a sufficiently large opening to the mantle cavity, which would otherwise be progressively restricted by the ontogenetic shell growth pattern of scaphopods. Decollation of the shell is necessary to achieve this change in shell shape, as direct dissolution of the aperture rim would be ineffective given the continuity of secondary shell secretion in *D. rectius*. Shell decollation has also been noted in several terrestrial gastropod families such as the Truncatellidae (MORRISON, 1963), Potamididae, Pleuroceridae (VERMEIJ, 1974), and Subulinidae (HOCHPÖCHLER & KOTHBAUER, 1975; KAT, 1981). Although also occurring in the marine Caecidae, the phenomenon is usually associated with tall-spired terrestrial species, found on hard substrates, in which the shell is wholly supported by the foot (VERMEIJ, 1974; KAT, 1981). The loss of one or more whorls is accomplished by dissolution of the internal shell surface, although eventual separation of the apex may be achieved through erosion of the weakened shell. The new apex is closed off or plugged by subsequent shell secretion (MORRISON, 1963; KAT, 1981). Removal of the shell apex is thought to increase the stability of the terrestrial snail by shifting the center of gravity to lie over the aperture; in contrast, gastropods that live in soft sediments have the shell supported in part by the substrate (VERMEIJ, 1974). In the terrestrial pulmonate gastropod *Rumina decollata*, the change in shell shape through loss of apical whorls has been related to increased mobility, reduction in shell weight, and reduced water loss, with a resultant increase in body and gonad size contributing to increased fitness (KAT, 1981). Although the immediate consequences of shell

decollation in *D. rectius* differ from those in terrestrial gastropods, it is a mechanism by which an otherwise severe restriction on growth is removed with a similar attendant potential for increasing fitness. In scaphopods of the genus *Cadulus* and other members of the Gadilida that do not secrete a secondary shell, posterior aperture increase could occur simply by shell dissolution at the aperture rim. In some species, there are several notches in the posterior aperture producing a lobate apex (ABBOTT, 1974), although the number of notches can be highly variable (SHIMEK, 1989). Removal of apical shell material in scaphopods can be considered one of several growth-related shell shape changes that molluscs achieve through shell dissolution or reabsorption, such as the enlargement of apical apertures in key-hole limpets (FRETTER & GRAHAM, 1962), removal of apertural spines in muricid gastropods (CARRIKER, 1972), internal remodelling of uppermost whorls in a variety of prosobranch gastropods (VERMEIJ, 1974), and surficial dissolution of the penultimate whorl in prosobranchs and *Nautilus* (SIGNOR, 1982, 1985).

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Repaired Shell Damage Among Soft-Bottom Mollusks on the Continental Shelf and Upper Slope North of Point Conception, California

by

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Abstract. The frequencies of repaired shell damage were estimated for univalved mollusks on the inner and outer continental shelf and upper slope in the Santa Maria Basin, north of Point Conception, California. Twenty-one percent of all gastropods and 18.7% of all examined scaphopods had repaired shell damage. The frequency of repaired shells among prosobranchs was significantly lower at upper slope stations than at either inner or outer shelf stations. Conversely, the frequency of repaired shells among scaphopods was significantly greater at upper slope stations than at inner shelf stations. Opisthobranchs showed no significant depth-related differences in repaired shell damage. The frequencies of shell repairs varied considerably among taxa. For example, the frequency of repaired damage was high for a scaphopod, *Cadulus tolmei* (47.2%), and for a prosobranch, *Alvinia rosana* (24.3%), but was low for eulimid gastropods (7.6%) and three species of *Epitonium* (no repaired shells).

INTRODUCTION

Within populations of mollusks it may be possible to infer the influence of shell-breaking predators by determining the frequency of repaired shell damage. Although nonlethal damage to shells may result from non-biological causes (SCHOENER, 1979), unsuccessful predation is thought to provide the most likely explanation for repaired shell damage (VERMEIJ, 1987). Repairs are easily recognizable as jagged discontinuities in the normal growth pattern of the shell (VERMEIJ, 1982; VALE & REX, 1988). The frequency of repaired shells in a population is known to be positively correlated with the incidence of unsuccessful attacks by predators (VERMEIJ, 1983). The importance of unsuccessful attacks by shell-breaking predators on the evolution of mollusks and the assumptions that must be considered in studies of such predation have been reviewed by VERMEIJ (1983, 1987).

Much of the information available regarding frequency of repaired shell damage among mollusks has resulted from the work of Vermeij on tropical snails (VERMEIJ, 1982; VERMEIJ *et al.*, 1980). From these studies the intensity of shell-breaking predation was inferred to be high and demonstrated to have profound effects on the evolution of molluscan shell architecture.

What is known about the phenomenon among mollusks from the temperate northeast Pacific comes from studies of rocky intertidal areas (FOTHERINGHAM, 1971; GELLER, 1983) or shallow subtidal environments (EDWARDS, 1969; BERGMAN *et al.*, 1983). These studies have shown that repair frequencies are generally lower in the temperate northeast Pacific than in tropical waters.

Little is known about the importance of shell-breaking predators in deep-water molluscan communities. The primary source of information comes from studies of shell repairs among deeper water molluscan communities in the northwest Atlantic by VALE & REX (1988, 1989). They found relatively low frequencies of repaired shell damage and suggested that predators on mollusks from deeper water communities were unspecialized.

A program designed to monitor the effects of offshore oil and gas development in the Santa Maria Basin, just north of Point Conception, California (HYLAND *et al.*, 1990b) provided the opportunity to investigate the extent of repaired shell damage among several groups of mollusks from the continental shelf and upper slope in the northeast Pacific. Large sample sizes permitted statistical analyses of the relationship of depth, small-scale latitudinal differences, and taxon to the frequency of repaired shell damage. The results of this investigation are presented here.

MATERIALS AND METHODS

The molluscan material used in this study was obtained during part of a program designed to assess potential long-term impacts of offshore oil and gas development in the southern Santa Maria Basin, California (HYLAND *et al.*, 1990b). Sediment samples were collected with a Hessler-Sandia 0.25-m² box corer partitioned into twenty-five 0.01-m² subcores. From each box-core sample the top 10 cm from 10 subcores was removed and processed for the analysis of the macroinfaunal community. The mollusks from these infaunal samples were used for this study. Details of the infaunal community analyses are reported in HYLAND *et al.* (1990a, in press). A voucher collection of all macroinfaunal taxa identified during the program, including the molluscan taxa investigated for repaired shell damage, will be deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC. Additionally, the bulk collection of the macroinfaunal specimens collected will be deposited in the Natural History Museum of Los Angeles County, Los Angeles, California.

The data were obtained from two sets of collections. The primary set, upon which the depth, transect, and taxonomic comparisons were based, was obtained from the sampling of 10 regional stations (designated R-1 through R-9 and PJ-1) situated along three cross-shelf transects (Figure 1). Three replicate samples were collected from each of the 10 regional stations on eight cruises between October 1986 and May 1989. Stations R-8 and R-9 were not sampled during the October 1986 cruise and Station R-7 was not sampled during the May 1988 cruise. Only two replicates were collected at Station R-3 during the May 1988 cruise. Of the 230 core samples collected, the mollusks from 212 (92%) were available to be examined for repaired shell damage.

The second set, used only to supplement the taxonomic comparisons, was obtained from 18 site-specific stations organized in a semi-radial array centered around Station PJ-1 (designated PJ-2 through PJ-23; see HYLAND *et al.*, 1990b). Of the 114 core samples collected from these stations, 99 (87%) were available for examination of the mollusks.

Because the molluscan fauna of the region has not been characterized, I used the data in appendix F-1 of HYLAND *et al.* (1990a) to describe briefly the univalved component of the community. Only taxa identified to species were used for these calculations. The top 10 prosobranch species, the top 20 opisthobranch species, and all six scaphopod species were included.

A dissection microscope was used to examine each mollusk for the presence of repair scars. Molluscan groups examined included prosobranch gastropods, pyramidellid and cephalasipdean opisthobranch gastropods, and scaphopods. All specimens within a sample were examined and scored for shell repair scars except those specimens too damaged by the collection process to evaluate. In the case of one abundant scaphopod species, *Cadulus californicus* Pilsbry & Sharp, 1898, so few specimens were usable that the species was not included in any observations. Re-

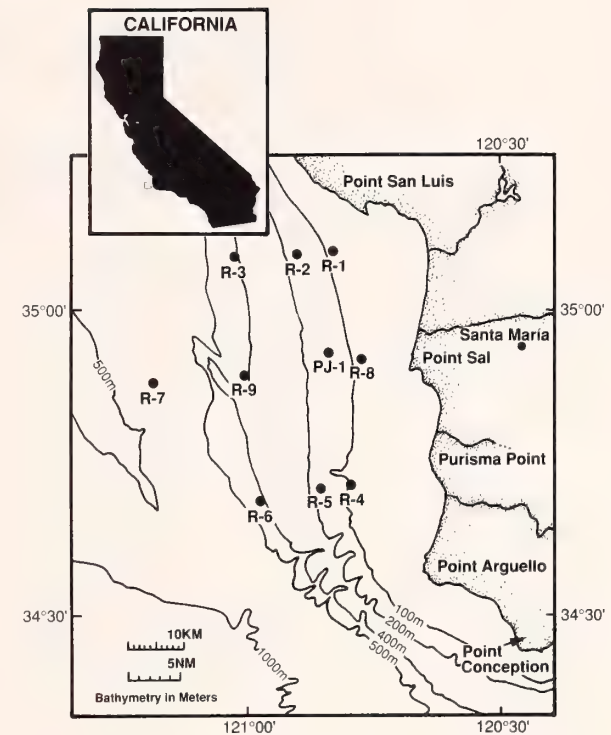


Figure 1

Map of the Santa Maria Basin, showing primary sampling locations.

paired damage in all groups was recognizable as irregular, usually jagged discontinuities in the normal growth pattern of the shell (*e.g.*, VERMEIJ, 1982; VALE & REX, 1988). Following VALE & REX (1988), repairs were recorded as major or minor, although all analyses were done using only the total number of repairs. The location and number of repairs on each shell were noted. For species of *Cadulus* (scaphopods) with repaired shells, the distance of the repair from the posterior aperture was measured with an ocular micrometer. The measure used as an indicator of shell repair in this study was the frequency of repaired shells (VALE & REX, 1988).

Three sets of statistical comparisons were done (chi-square 2×2 tables; SOKAL & ROHLF, 1981) using various groupings of the stations listed in Table 1. First, a comparison of the effect of depth was tested. Three depth categories were established; inner shelf (Stations R-1, R-8, R-4; depth 90–91 m), outer shelf (Stations R-2, PJ-1, R-5; depth 145–161 m), and upper slope (Stations R-3, R-6, R-7, R-9; depth 409–565 m). Second, the effect of “latitudinal” position on the frequency of shell repair was tested by grouping the stations into three transects: north (Stations R-1, R-2, R-3; ca. 35°05’N), middle (Stations R-8, PJ-1, R-9; ca. 34°55’N), and south (Stations R-4,

Table 1

Station data for samples used in comparisons of depth and transect effects on the frequency of repaired shells among each taxonomic category. No is the north transect, So is the south transect, Mi is the middle transect, *n* is the number of specimens examined, % is the percent of the shells having repair scars.

Sta.	Transect	Depth (m)	Prosobranchs		Opisthobranchs		Scaphopods		Total fauna	
			<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
R-1	No	91	58	17.2	69	21.7	55	9.1	182	16.5
R-2	No	161	97	16.5	118	11.9	44	29.6	259	16.6
R-3	No	409	30	16.7	7	57.1	38	18.4	75	21.3
R-4	So	92	482	28.4	41	36.6	45	13.3	568	27.8
R-5	So	154	34	11.8	22	45.4	7	28.6	63	25.4
R-6	So	410	233	14.6	18	11.1	49	26.5	300	16.3
R-7	—	565	27	7.4	0	—	2	0	29	6.9
R-8	Mi	90	78	11.5	174	16.1	37	16.2	289	14.9
R-9	Mi	410	138	11.6	0	—	14	57.1	152	15.8
PJ-1	Mi	145	495	23.4	33	12.1	31	3.2	559	21.6

R-5, R-6; ca. 34°42'N). Although relatively close together, these three transects have been shown to differ somewhat in the structure of their infaunal communities (HYLAND *et al.*, 1990a, in press). Last, two sets of taxonomic comparisons were made. First, differences in the frequency of repaired shells were compared among five taxonomic categories: an abundant small prosobranch, *Alvinia rosana* (Bartsch, 1911), all other prosobranchs, pyramidellidan opisthobranchs, cephalasipdean opisthobranchs, and scaphopods. Second, the large sample sizes available allowed for comparisons to be done on a finer scale within each of the major groups. Involved were selected comparisons between families, genera, species, or groups of each taxonomic category. All available data were used for the taxonomic comparisons.

RESULTS AND DISCUSSION

The Univalved Mollusk Fauna

The univalved mollusks collected during the program were mostly small species, having maximum sizes smaller than 10 to 15 mm in length (ABBOTT, 1974). Prosobranch gastropods were the predominant univalves for the two shelf regions, having densities of 93 and 119 individuals/m² for the inner and outer shelf stations, respectively. *Alvinia rosana* (Rissoidae) was the most common gastropod on the shelf, reaching densities of 192 individuals/m² at Station R-4 (inner shelf) and 273 individuals/m² at Station PJ-1 (outer shelf). *Alvinia rosana* was not found at any upper slope station. A turrid, *Kurtziella beta* (Dall, 1919), was the second-most abundant species on the inner shelf, reaching a peak density of 23 individuals/m² at Station R-8. The eulimid *Balcis rutila* (Carpenter, 1864), with a peak density of 12 individuals/m² at Station PJ-1, was the second-ranked prosobranch on the outer shelf. The upper slope was characterized by relatively high abundances of *Amphissa bicolor* Dall, 1892, which reached 65

and 70 individuals/m² at Stations R-9 and R-6, respectively, and *Bittium fetellum* Bartsch, 1911, which reached 64 individuals/m² at Station R-6.

Opisthobranchs declined in abundance with increasing depth. Most common on the inner shelf were *Cylichna diegensis* (Dall, 1919), occurring at densities of 23 individuals/m² at Station R-8, and *Volvulella panamica* Dall, 1919, found at 12 to 15 individuals/m² at Stations R-1 and R-8, respectively. *Odostomia pratoma* Dall & Bartsch, 1909, and *O. phanella* Dall & Bartsch, 1909, were the most common opisthobranchs on the outer shelf, occurring at densities of 17 and 18 individuals/m², respectively. Opisthobranchs were rare on the upper slope, occurring at only Stations R-3 and R-6 at densities of 2 and 7 individuals/m², respectively.

Scaphopods were the predominant univalved mollusks on the upper slope, where their densities ranged from 53 to 214 individuals/m². Common upper slope species were *Cadulus californicus* (22 to 197 individuals/m²) and *C. tolmei* Dall, 1897 (up to 19 individuals/m²). Scaphopods were less common on the shelf, although *Siphonodentalium quadrifissatum* (Pilsbry & Sharp, 1898) was particularly numerous on the inner shelf (30 individuals/m²).

Repaired Shell Damage

The number of specimens examined and the frequency of repair for each major taxonomic category occurring at the primary stations are listed in Table 1. All raw data including the species examined, taxonomic authorities, number of specimens examined, the number repaired, as well as the depth and location for all stations, are listed in the Appendix. Over all depths and transects, 21.0% of the gastropod shells examined and 18.7% of the scaphopods examined were repaired. Major repairs accounted for 93.5% of all repairs counted. Of the 1026 shells having repairs, only 11 (1.1%) had more than one repair. Among gastro-

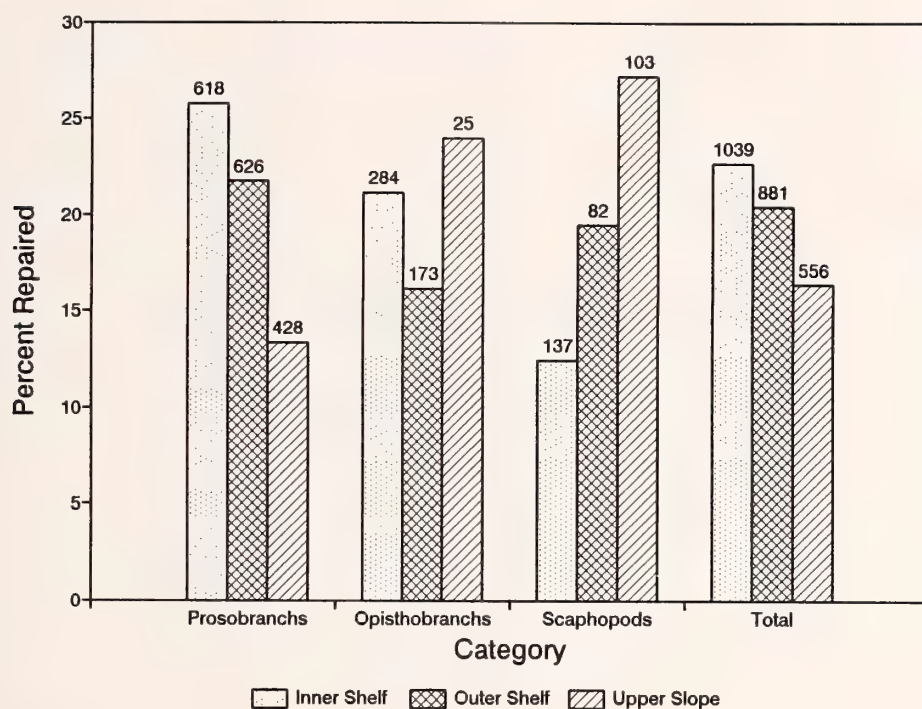


Figure 2

The percentage of prosobranch, opisthobranch, and scaphopod mollusks with repaired shell damage for each depth category.

pods, 21.8% of the prosobranchs and 16.3% of the opisthobranchs were repaired. The percent repaired found for opisthobranchs may be a conservative estimate because many of the species examined were cephalaspideans, most of which have the early whorls obscured by the body whorl. Most repairs on gastropod shells were located on the body whorl, although the exact number was not determined.

Depth and Transect Comparisons

The percentages of shells having repairs at each of the three depth categories are shown in Figure 2 and the results of the Chi-square tests in Table 2. Although the frequency of repair of prosobranchs decreased with increasing depth, the only significant differences detected were between the

Table 2

Results of chi-square 2×2 test comparing the frequency of shell repairs between pairs of depth category for each major taxonomic group.

<i>Prosobranchs</i>			<i>Opisthobranchs</i>		
	Outer shelf	Upper slope		Outer shelf	Upper slope
Inner shelf	2.75	23.77***	Inner shelf	1.69	0.11
Outer shelf		12.01***	Outer shelf		0.94
<i>Scaphopods</i>			<i>Total</i>		
	Outer shelf	Upper slope		Outer shelf	Upper slope
Inner shelf	2.02	8.43**	Inner shelf	1.46	8.95**
Outer shelf		1.48	Outer shelf		3.68

** Significant χ^2 value at $\alpha = 0.01$.

*** Significant χ^2 value at $\alpha = 0.001$.

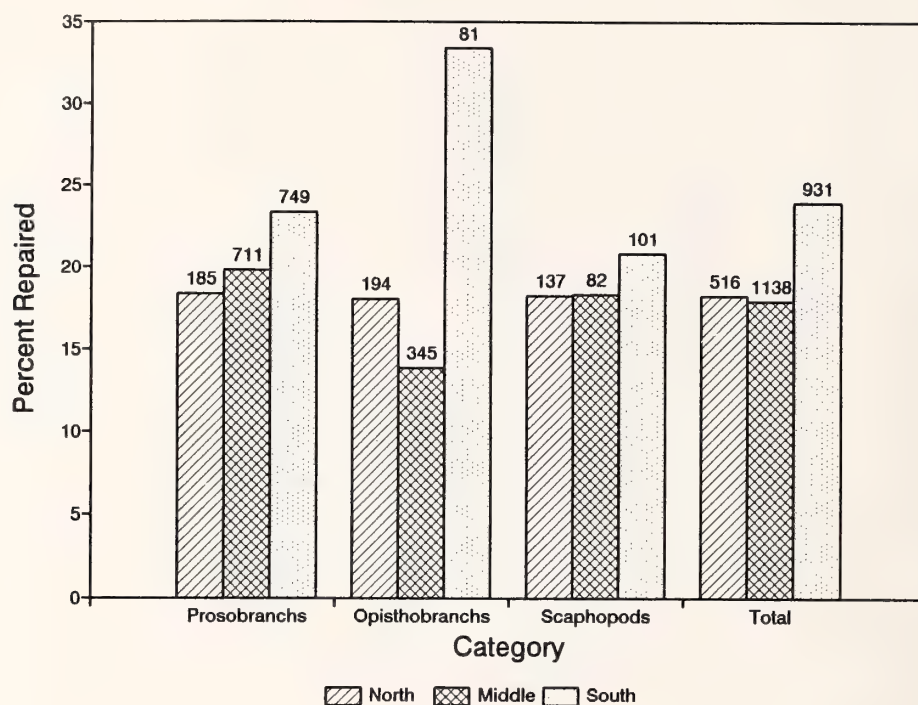


Figure 3

The percentage of prosobranch, opisthobranch, and scaphopod mollusks with repaired shell damage for each transect.

upper slope stations and both the inner shelf and outer shelf stations.

However, conclusions regarding the frequency of repair not only reflect the level of predation within a particular depth regime, but they also necessarily reflect the composition of the resident molluscan fauna. That the repair frequency is relatively low on the upper slope does not

mean that it is low for all taxa present. Note that at upper slope stations species of *Bittium* show a fairly high incidence of repair (24.2%, $n = 95$), whereas *Amphissa bicolor* and *Astyris permodesta* (Dall, 1890) had a combined rate of 10.5% ($n = 314$). Similarly, the relatively high rate of repair at shelf locations might be explained by the high abundance of *Alvinia rosana*, a species that has a relatively

Table 3

Results of chi-square tests comparing the frequency of repaired shells between pairs of transects for each major taxonomic category.

<i>Prosobranchs</i>			<i>Opisthobranchs</i>		
	Middle transect	South transect		Middle transect	South transect
North transect	0.20	2.12	North transect	1.62	7.65**
Middle transect		2.68	Middle transect		17.06***
<i>Scaphopods</i>			<i>Total</i>		
	Middle transect	South transect		Middle transect	South transect
North transect	<0.01	0.24	North transect	0.02	6.38*
Middle transect		0.18	Middle transect		11.36***

* Significant χ^2 value at $\alpha = 0.05$.

** Significant χ^2 value at $\alpha = 0.01$.

*** Significant χ^2 value at $\alpha = 0.001$.

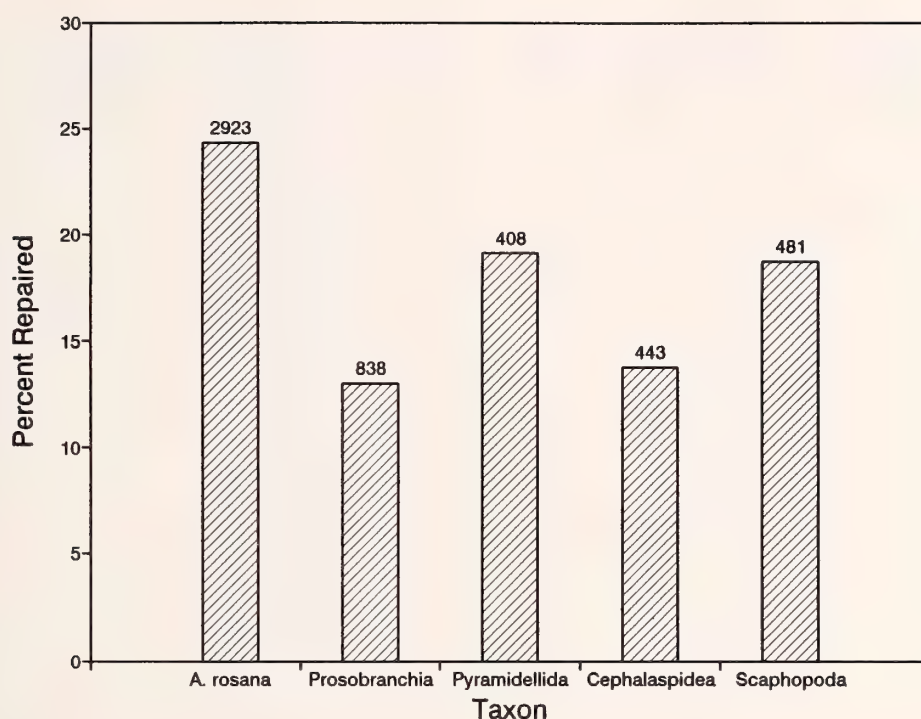


Figure 4

The percentage of repaired shells among each of the major taxonomic categories. The category Prosobranchia excludes *Alvinia rosana*.

high repair rate (24.3%, $n = 2923$). Other shelf taxa, for example species of *Epitonium*, had very low repair rates (no repairs, $n = 32$).

The trend found for scaphopods was opposite to that of prosobranchs, as repaired shells increased in frequency with depth, although the only significant difference was between the inner shelf and the upper slope. The repair frequencies observed for scaphopods at upper slope stations reflect the level of predation on a portion of the scaphopod population present because the predominant species occurring on the slope, *Cadulus californicus*, was too damaged by the collection process to evaluate. Opisthobranchs showed no significant depth-related differences in the frequency of repaired shells.

The frequencies of shell repairs for each transect are shown in Figure 3. Among the three major taxonomic categories there was a weak trend for the south transect to have higher proportions of shells having repairs than either of the other two transects. However, opisthobranchs showed the only significant differences; the south transect (33.3% repaired) differed from the north transect (18.0%) and the middle transect (13.9%; Table 3). The total univalve fauna also showed significant differences between the south transect (24.0%) and either the north transect (18.2%) or the middle transect (17.9%). There is no immediate explanation for the significantly greater repair

frequency shown by opisthobranchs on the southern transect as compared to the other two.

Taxonomic Comparisons

The frequencies of repaired shells found among the five taxonomic categories examined are shown in Figure 4. The percentage of shells repaired for *Alvinia rosana* (24.3%) was significantly greater than those for any other group (Table 4). As a contrast to *A. rosana*, the frequency of

Table 4

Results of chi-square 2×2 tests comparing the frequency of repaired shells between pairs of taxonomic categories.

	Proso- branchia ^a	Pyrami- dellida	Cephala- spidea	Scaph- opoda
<i>Alvinia rosana</i>	48.93***	5.37*	24.25***	7.23**
Prosobranchia ^a		8.03**	0.15	7.76**
Pyramidellida			4.44*	0.02
Cephalaspidea				4.12*

^a Excluding *Alvinia rosana*.

* Significant χ^2 value at $\alpha = 0.05$.

** Significant χ^2 value at $\alpha = 0.01$.

*** Significant χ^2 value at $\alpha = 0.001$.

repair was only 13.0% for all other prosobranchs. Among the other possible comparisons, all showed significant differences except prosobranchs (excluding *A. rosana*) versus cephalaspideans and pyramidellidans versus scaphopods (18.7%; Table 4).

Prosobranchs: The frequency of repair varied considerably among prosobranchs, even within the same general sampling regime. For example, species of *Epitonium* in the study area had no repairs ($n = 32$), whereas the high-spined, but relatively unarmored, species of *Bittium* had 24.8% with repairs ($n = 109$), including one specimen with four repairs. The two predominant species of the family Eulimidae collected, *Balcis rutila* and *B. micans* (Carpenter, 1864), did not differ in the frequency of repaired shells ($\chi^2 < 0.01$, $P = 0.97$, $n = 165$). Similarly, the two predominant species of the family Turridae collected, *Kurtziella beta* and *Kurtzia arteaga* (Dall & Bartsch, 1910), did not differ in repair frequency ($\chi^2 = 0.42$, $P = 0.52$, $n = 175$). However, a comparison between turrids (16.6%, $n = 177$) and eulimids (7.6%, $n = 170$) did show a significant difference in the repair frequency ($\chi^2 = 6.91$, $P < 0.01$). Shell morphology may help explain the differences. Relatively high repair rates were found among small, thin-shelled species (*Alvinia rosana*) and some high-spined species (*Bittium* spp.). Rates were low for heavily sculptured species (*Epitonium* spp.) or very smooth-shelled species (*Balcis* spp.). VERMEIJ (1987) predicted that several morphological features of gastropod shells may be effective deterrents to predation. These include narrow apertures, heavy sculpture, and tall spires that permit substantial withdrawal of the snail body into the shell. Three of the examples of predation rates mentioned above seem to contradict Vermeij's predictions. However, two of the taxa, *Epitonium* and *Balcis*, may be less susceptible to predation because they are symbionts of cnidarians and echinoderms, respectively, which may reduce the likelihood of detection by a predator. Relevant to *Balcis*, WARÉN (1984) observed repair scars on species of eulimids and speculated that the smooth shell may make it difficult for a predator to grasp the shell. *Alvinia rosana*, a very small rissoid (length up to 2.6 mm; ABBOTT, 1974), would seem not to offer much resistance to a shell-breaking predator. However, small size may limit the maximum size of a potential predator. The relatively high incidence of repaired damage found for *Alvinia* may indicate that the most influential predators on these snails were relatively small (e.g., crangonid shrimp). The frequency of repair scars found here for *Alvinia* was similar to the highest values found by VALE & REX (1989) for upper continental slope rissoids in the northwest Atlantic.

Opisthobranchs: Among opisthobranchs, pyramidellidans (19.1%) had a significantly higher frequency of repairs than cephalaspideans (13.8%; Table 4). Two possible explanations may be given for the differences in repair rates between cephalaspideans and pyramidellidans. First,

the repair rates for the former may have been underestimated because repairs occurring on early whorls may become obscured by the body whorl as the snail grows. Second, the high rates found for the latter group may reflect the relatively high-spined shells found within that group. Among pyramidellid opisthobranchs, the proportion of repaired shells for species of *Turbonilla* (27.6%, $n = 134$) differed significantly from species of *Odostomia* (12.8%, $n = 258$; $\chi^2 = 13.21$, $P < 0.001$). This difference does not appear to be a result of a difference in spatial distribution because the two genera co-occur throughout the Santa Maria Basin. *Turbonilla* is a typically higher-spined, more heavily sculptured taxon than *Odostomia*, features that contribute to greater resistance to shell-breaking predators (VERMEIJ, 1983, 1987). Two repair scars were found on each of four pyramidellid specimens. No significant differences were detected among various comparisons of cephalaspidean genera ($\chi^2 = 0.01$ to 3.14, $P = 0.08$ to 0.93, $n = 137$ to 239).

Scaphopods: Differences in the frequency of repaired shell damage between the predominant species found on the inner shelf (*Siphonodentalium quadrifissatum*; 14.9%, $n = 335$) and that found on the upper slope (*Cadulus tolmei*; 47.2%, $n = 53$) were significant ($\chi^2 = 30.51$, $P \ll 0.001$). Both are similar in size, shell surface texture, and morphology (SHIMEK, 1989). Of the indices proposed by Shimek, only the whorl expansion rate showed a significant difference between the two species. Shimek hypothesized that the shell morphology of these species may allow relatively fast burrowing, which may permit escape from potential predators. If the rate of burrowing does affect the ability to escape, then differences in the sediment composition of the substrate that affect burrowing rate may explain differences in the intensity of predation observed between the two populations. Within the Santa Maria Basin, sediments at the shelf stations generally are coarser than those at the upper slope stations (KINNEY *et al.*, 1990) although Station R-6 is an exception to this trend. The finer sediments on the upper slope may be more difficult to burrow through, thereby reducing the ability of the resident scaphopods to escape predators. A comparison of the genus *Dentalium* (14.5%, $n = 83$) with *Cadulus*/*Siphonodentalium* (19.4%, $n = 397$) showed no significant differences between the two ($\chi^2 = 1.11$, $P = 0.29$).

Most (54%) repair scars on species of *Cadulus*/*Siphonodentalium* occurred within 2 mm of the posterior aperture, although there was a second peak in the frequency of repair at a distance of 9 mm from the aperture (Figure 5). This would indicate that predation intensity is greater on juveniles than adults although this requires the assumption that the damage was done to the lip of the anterior aperture. Juveniles are thought to be less capable burrowers than adults (SHIMEK, 1989). The second peak in frequency of repairs may indicate that the risk of a predatory attack may be greater as adults move toward the surface of the sediment to reproduce (SHIMEK, 1989).

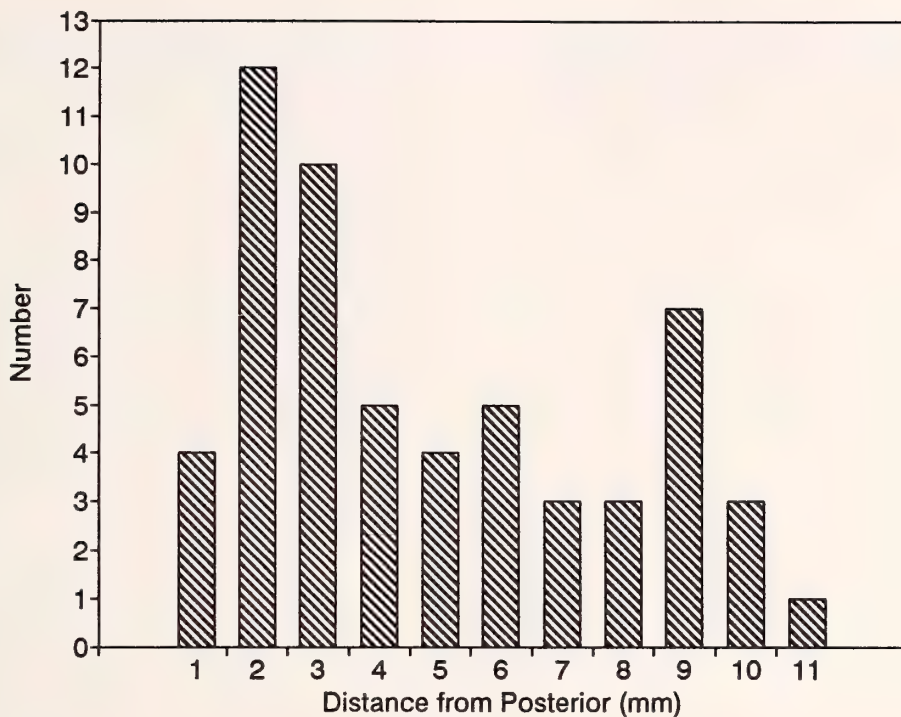


Figure 5

The distance of repaired shell damage from the posterior aperture of species of *Cadulus/Siphonodentalium*.

The frequencies of repaired shell damage reported here differ with the information concerning predation on scaphopods provided by SHIMEK (1989) although he did not provide quantitative data. Shimek reported that repaired damage is rare for *Cadulus aberrans* Whiteaves, 1887, but higher for other species, including *Dentalium rectius*. Shimek also found species of *Cadulus* to be rare in the stomachs of ratfish (*Hydrolagus collii*), whereas other scaphopods were common.

Comparisons with Other Regions

The difficulties in making comparisons among regions and studies have been noted by VALE & REX (1988). However, by using only the number of major repairs encountered, the results presented here can be compared directly with VALE & REX (1988). Also, the results from the Santa Maria Basin, in which only 1% of the repaired shells had multiple repairs, can be roughly compared to the average number of scars per shell used in other studies (e.g., VERMEIJ, 1982; VERMEIJ *et al.*, 1980).

For prosobranchs, the depth-related differences observed here, in which the frequency of repaired shells decreases with the increase in depth from shelf stations to upper slope stations, contrasts with the pattern in the northwest Atlantic. VALE & REX (1988) found repair frequencies to increase with depth from shelf to upper slope, though the difference between the two areas was not sta-

tistically significant. The range of frequencies of major repairs for shelf habitats was higher in the Santa Maria Basin (10.3–25.9%) than in the northwest Atlantic (4%). For upper slope habitats the ranges found for the two regions were similar: 3.7–13.3% in the Santa Maria Basin and 8–14% in the northwest Atlantic.

Comparisons between the results of this study with those focusing on other northeast Pacific mollusks may not be particularly useful because of the differences in the taxa considered by each study. However, it seems that predation by shell-breakers on some members of the soft-bottom Santa Maria Basin fauna is less important as an agent of selection than it is for some intertidal mollusks (FOTHERINGHAM, 1971; GELLER, 1983) or some populations of shallow, subtidal soft-bottom mollusks (BERGMAN *et al.*, 1983).

The overall repair frequency found among prosobranchs off California, if calculated as the average number of scars per shell (0.21; 820 single scars + 6 multiple scars, $n = 3761$), was generally lower than those found for soft-bottom habitats in tropical waters. VERMEIJ (1982) found the average number of scars per shell to range from 0 to 2.23 for tropical communities in the Pacific.

Literature records of repair scars among opisthobranchs are scanty. VERMEIJ (1982) lists results for two pyramidellid genera, *Otopleura* and *Pyramidella*, from Guam. Repair frequencies (measured as average number of scars per shell) for those taxa ranged from 0.23 to 0.62. These values

compare to the 0.18 scars per shell recorded for pyramidellids from the Santa Maria Basin (70 single repairs + 4 multiple scars = 74 total scars, $n = 392$). I have not been able to find any literature records of repair frequencies for scaphopods from other regions with which to compare directly the results from the Santa Maria Basin study.

Predation on Univalved Mollusks in the Santa Maria Basin

The types of predators most likely to affect the evolution of univalved mollusks have been reviewed by VERMEIJ (1987) and summarized for continental shelf soft-bottom mollusks by VALE & REX (1988). Little information is available for the predators present in the Santa Maria Basin. Most larger predators were rarely sampled during this program (refer to appendix F-1 in HYLAND *et al.*, 1990a, for taxa collected). A few decapods, such as crangonid shrimp and juvenile *Cancer*, that may prey on mollusks were collected. Among the fish likely to prey on mollusks, the ratfish (*Hydrolagus collieri*) and several species of sculpins (Cottidae) have geographic and depth ranges at least partially overlapping those of the study area (MILLER & LEA, 1972). Ratfish prey on scaphopods (SHIMEK, 1989) and shallow-water cottids feed on small rissoinid snails, inflicting a distinctive pattern of damage to the shell (NORTON, 1988). Several taxa of echinoderms may ingest molluscan prey without damaging the shells (CAREY, 1972; PEARSON & GAGE, 1984). During this program a molluscivorous asteroid, *Astropecten verrilli* (Fisher, 1906), was collected rarely. Some species of brittlestars, *Ophiura* spp., ingest gastropods whole (PEARSON & GAGE, 1984). *Ophiura* was uncommon in the Santa Maria Basin. One abundant polychaete in the Santa Maria Basin, *Chloea pinnata* Moore, 1911, was found to have an intact *Alvinia rosana* in its digestive tract.

Unsuccessful predatory attacks on the molluscan fauna of the Santa Maria Basin do occur. However, the incidence of these attacks, as measured by the frequency of repaired shell damage, is relatively low. It seems likely that in the Santa Maria Basin, as found by VALE & REX (1988) for the northwest Atlantic, the predators on mollusks are generalists and have not had a major influence on the evolution of the resident fauna.

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APPENDIX

Raw shell repair data. Taxonomic authorship is provided at the first occurrence of each species.

Locality and species	<i>n</i>	Major repairs	Minor repairs	Total repairs
Station R-1 [35°05.8'N, 120°49.2'W; 91 m]				
<i>Alvinia rosana</i> (Bartsch, 1911)	21	4	0	4
<i>Balcis rutila</i> Carpenter, 1864	1	0	0	0
<i>Caecum crebricinctum</i> Carpenter, 1864	1	0	0	0
<i>Epitonium</i>	2	0	0	0
<i>Epitonium caamanoi</i> Dall & Bartsch, 1910	2	0	0	0
<i>Epitonium sawinae</i> (Dall, 1903)	1	0	0	0
<i>Kurtzia arteaga</i> (Dall & Bartsch, 1910)	7	2	0	2
<i>Kurtziella beta</i> (Dall, 1919)	23	4	3	7
<i>Odostomia pratoma</i> Dall & Bartsch, 1909	1	0	0	0
<i>Odostomia dinella</i> Dall & Bartsch, 1909	7	4	0	4
<i>Turbonilla</i>	2	0	0	0
<i>Turbonilla raymondi</i> Dall & Bartsch, 1909	1	0	0	0
<i>Turbonilla newcombei</i> Dall & Bartsch, 1907	1	0	0	0
<i>Turbonilla santarosana</i> Dall & Bartsch, 1909	2	1	0	1
<i>Turbonilla</i> (<i>Chemnitzia</i>) sp. A	2	0	0	0
<i>Turbonilla</i> (<i>Chemnitzia</i>) sp. F	3	2	0	2
<i>Turbonilla</i> (<i>Pyrgiscus</i>) sp. A	2	0	0	0
<i>Cylichna diegensis</i> (Dall, 1919)	13	5	1	6
<i>Volvulella cylindrica</i> (Carpenter, 1864)	10	1	0	1
<i>Volvulella panamica</i> Dall, 1919	16	2	1	3
<i>Sulcoretusa xystrum</i> (Dall, 1919)	9	0	0	0
<i>Siphonodentalium quadrifissatum</i> (Pilsbry & Sharp, 1898)	55	5	0	5
Station R-2 [35°05.5'N, 120°53.4'W; 161 m]				
<i>Alvinia rosana</i>	56	9	1	10
<i>Amphissa bicolor</i> Dall, 1892	3	0	0	0
<i>Antiplanes</i>	1	1	0	1
<i>Balcis</i>	1	0	0	0
<i>Balcis micans</i> Carpenter, 1864	5	1	0	1
<i>Balcis rutila</i>	20	1	1	2
<i>Bittium fetellum</i> Bartsch, 1911	2	1	0	1
<i>Bittium quadrifilatum</i> Carpenter, 1864	1	1	0	1
<i>Boreotrophon</i> sp. 1	1	0	0	0
<i>Epitonium lowei</i> (Dall, 1906)	2	0	0	0
<i>Kurtzia arteaga</i>	1	0	0	0
<i>Kurtziella beta</i>	4	0	0	0
<i>Odostomia dinella</i>	5	0	0	0
<i>Odostomia jewetti</i> Dall & Bartsch, 1907	8	0	0	0
<i>Odostomia phanella</i> Dall & Bartsch, 1909	43	3	2	5
<i>Odostomia pratoma</i>	41	3	2	5
<i>Odostomia tenuisculpta</i> Carpenter, 1864	2	1	0	1
<i>Turbonilla</i>	7	0	0	0
<i>Turbonilla newcombei</i>	1	0	0	0
<i>Turbonilla raymondi</i>	1	0	0	0
<i>Turbonilla</i> (<i>Chemnitzia</i>) sp. F	1	1	0	1
<i>Cylichna diegensis</i>	2	1	0	1

APPENDIX

Continued.

Locality and species	<i>n</i>	Major repairs	Minor repairs	Total repairs
<i>Cylichnella culcitella</i> (Gould, 1852)	3	1	0	1
<i>Cylichnella harpa</i> (Dall, 1871)	4	0	0	0
<i>Siphonodentalium quadrifissatum</i>	28	10	0	10
<i>Dentalium rectius</i> Carpenter, 1864	16	3	0	3
Station R-3 [35°05.3'N, 121°00.9'W; 409 m]				
<i>Alaba</i> nr. <i>supralirata</i>	1	0	0	0
<i>Amphissa bicolor</i>	30	4	1	5
<i>Balcis rutila</i>	1	0	0	0
<i>Odostomia pratoma</i>	1	0	0	0
<i>Turbonilla</i>	2	2	0	2
<i>Turbonilla</i> (<i>Chemnitzia</i>) sp. A	3	2	0	2
<i>Cadulus tolmei</i> Dall, 1897	11	4	1	5
<i>Dentalium rectius</i>	20	2	0	2
<i>Dentalium vallicolens</i> Raymond, 1904	7	0	0	0
Station R-4 [34°43.0'N, 120°47.4'W; 92 m]				
<i>Alvinia rosana</i>	428	119	12	131
<i>Balcis rutila</i>	2	0	0	0
<i>Cancellaria crawfordiana</i> (Dall, 1891)	1	0	0	0
<i>Epitonium caamanoi</i>	2	0	0	0
<i>Epitonium lowei</i>	1	0	0	0
<i>Epitonium sawinae</i>	6	0	0	0
<i>Kurtzia arteaga</i>	15	2	0	2
<i>Kurtziella beta</i>	20	2	0	2
<i>Mitrella</i>	5	1	0	1
Turridae sp. 1	2	1	0	1
<i>Cyclostremella</i> sp. A	16	7	1	8
<i>Odostomia</i>	1	0	1	1
<i>Odostomia dinella</i>	3	2	0	2
<i>Turbonilla</i>	1	1	0	1
<i>Turbonilla ambusta</i> Dall & Bartsch, 1909	1	1	0	1
<i>Turbonilla newcombei</i>	1	0	0	0
<i>Turbonilla santarosana</i>	1	0	0	0
<i>Turbonilla</i> (<i>Pyrgiscus</i>) sp. A	2	1	0	1
<i>Cylichna diegensis</i>	2	0	0	0
<i>Cylichnella culcitella</i>	2	0	0	0
<i>Cylichnella harpa</i>	1	1	0	1
<i>Sulcoretusa xystrum</i>	2	0	0	0
<i>Volvulella cylindrica</i>	6	0	0	0
<i>Volvulella panamica</i>	2	0	0	0
<i>Siphonodentalium quadrifissatum</i>	45	6	0	6
Station R-5 [34°42.7'N, 120°50.8'W; 154 m]				
<i>Alvinia rosana</i>	9	2	0	2
<i>Balcis micans</i>	2	0	0	0
<i>Balcis rutila</i>	14	1	0	1
<i>Epitonium</i>	1	0	0	0
<i>Epitonium sawinae</i>	3	0	0	0
<i>Eulima californica</i> (Bartsch, 1911)	1	0	0	0
<i>Kurtziella beta</i>	3	0	0	0
<i>Simnia</i> sp. 1	1	1	0	1
<i>Turbonilla</i>	4	2	0	2
<i>Turbonilla ambusta</i>	1	0	0	0
<i>Turbonilla newcombei</i>	3	3	0	3
<i>Turbonilla santarosana</i>	4	2	0	2
<i>Turbonilla</i> (<i>Chemnitzia</i>) sp. F	1	1	0	1
<i>Cylichna diegensis</i>	5	1	0	1
<i>Cylichnella culcitella</i>	1	1	0	1

APPENDIX

Continued.

Locality and species	<i>n</i>	Major repairs	Minor repairs	Total repairs
<i>Cylichnella harpa</i>	2	0	0	0
<i>Volvulella cylindrica</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	6	1	0	1
<i>Dentalium vallicolens</i>	1	1	0	1
Station R-6 [34°41.4'N, 120°57.9'W; 410 m]				
<i>Alaba</i> nr. <i>supralirata</i>	7	2	0	2
<i>Amphissa bicolor</i>	134	9	3	12
<i>Bittium attenuatum</i> Carpenter, 1864	2	2	0	2
<i>Bittium fetellum</i>	87	16	2	18
<i>Bittium</i> sp. A	3	0	0	0
<i>Turbonilla</i>	5	1	0	1
<i>Turbonilla newcombei</i>	10	1	0	1
<i>Turbonilla</i> (<i>Chemnitzia</i>) sp. A	2	0	0	0
<i>Volvulella panamica</i>	1	0	0	0
<i>Cadulus tolmei</i>	32	11	2	13
<i>Dentalium rectius</i>	6	0	0	0
<i>Dentalium vallicolens</i>	11	0	0	0
Station R-7 [34°52.9'N, 121°10.3'W; 565 m]				
<i>Astyris permodesta</i> (Dall, 1890)	27	1	1	2
<i>Dentalium rectius</i>	2	0	0	0
Station R-8 [34°55.3'N, 120°45.9'W; 90 m]				
<i>Alvinia rosana</i>	8	1	0	1
<i>Amphissa bicolor</i>	1	0	0	0
<i>Balcis micans</i>	1	0	0	0
<i>Balcis rutila</i>	2	0	0	0
<i>Epitonium lowei</i>	1	0	0	0
<i>Epitonium sawinae</i>	3	0	0	0
<i>Kurtzia arteaga</i>	14	2	0	2
<i>Kurtziella beta</i>	45	4	1	5
<i>Trochidae</i> sp. 1	2	1	0	1
<i>Vitrinella oldroydi</i> Bartsch, 1907	1	0	0	0
<i>Odostomia dinella</i>	2	0	0	0
<i>Turbonilla</i>	4	1	0	1
<i>Turbonilla aepynota</i> Dall & Bartsch, 1909	1	0	0	0
<i>Turbonilla ambusta</i>	1	1	0	1
<i>Turbonilla raymondi</i>	2	1	0	1
<i>Turbonilla santarosana</i>	7	1	0	1
<i>Turbonilla</i> (<i>Chemnitzia</i>) sp. F	12	6	0	6
<i>Turbonilla</i> (<i>Pyrgiscus</i>) sp. A	3	0	0	0
<i>Cylichna diegensis</i>	43	4	1	5
<i>Cylichnella culcitella</i>	7	2	0	2
<i>Cylichnella harpa</i>	2	0	0	0
<i>Volvulella cylindrica</i>	33	2	1	3
<i>Volvulella panamica</i>	26	4	0	4
<i>Sulcoretusa xystrum</i>	31	2	2	4
<i>Cadulus fusiformis</i>	6	2	0	2
<i>Siphonodentalium quadrifissatum</i>	30	3	0	3
<i>Dentalium</i> sp. 1	1	1	0	1
Station R-9 [34°53.7'N, 120°59.1'W; 410 m]				
<i>Admete rhyssa</i> (Dall, 1919)	2	0	0	0
<i>Amphissa bicolor</i>	120	10	5	15
<i>Balcis micans</i>	6	0	0	0
<i>Balcis rutila</i>	4	0	0	0
<i>Bittium fetellum</i>	3	3	3	3
<i>Astyris permodesta</i>	3	1	0	1

APPENDIX

Continued.

Locality and species	<i>n</i>	Major repairs	Minor repairs	Total repairs
<i>Cadulus tolemi</i>	10	6	1	7
<i>Dentalium rectius</i>	1	0	0	0
<i>Dentalium vallicolens</i>	3	1	0	1
Station PJ-1 [34°55.8'N, 120°49.9'W; 145 m]				
<i>Alvinia rosana</i>	455	96	14	110
<i>Balcis micans</i>	3	0	0	0
<i>Balcis rutila</i>	22	0	0	0
<i>Bittium</i> sp. A	1	1	0	1
<i>Epitonium</i>	1	0	0	0
<i>Eulima californica</i>	1	1	0	1
<i>Kurtzia arteaga</i>	2	0	0	0
<i>Kurtziella beta</i>	10	3	1	4
<i>Odostomia</i>	1	0	1	1
<i>Odostomia dinella</i>	12	0	0	0
<i>Odostomia phanella</i>	1	0	0	0
<i>Turbonilla ambusta</i>	2	0	0	0
<i>Cylichna diegensis</i>	3	1	1	2
<i>Cylichnella culcitella</i>	6	1	1	2
<i>Cylichnella harpa</i>	4	0	0	0
<i>Diaphana californica</i> Dall, 1919	2	1	0	1
<i>Volvulella panamica</i>	2	0	0	0
<i>Cadulus fusiformis</i>	2	0	0	0
<i>Siphonodentalium quadrifissatum</i>	29	1	0	1
Station PJ-2 [34°55.3'N, 120°49.6'W; 142 m]				
<i>Alvinia rosana</i>	14	3	0	3
<i>Balcis rutila</i>	1	0	0	0
<i>Kurtzia arteaga</i>	1	0	0	0
<i>Turbonilla ambusta</i>	2	0	0	0
<i>Turbonilla santarosana</i>	1	0	0	0
<i>Turbonilla</i> (Chemnitzia) sp. F	1	0	0	0
<i>Volvulella cylindrica</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	4	0	0	0
Station PJ-3 [34°56.3'N, 120°49.6'W; 138 m]				
<i>Alvinia rosana</i>	21	6	0	6
<i>Balcis micans</i>	1	1	0	1
<i>Balcis rutila</i>	2	0	0	0
<i>Odostomia dinella</i>	1	0	0	0
<i>Volvulella panamica</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	5	0	0	0
Station PJ-4 [34°56.3'N, 120°50.2'W; 150 m]				
<i>Alvinia rosana</i>	28	4	1	5
<i>Balcis rutila</i>	3	0	0	0
<i>Kurtziella beta</i>	1	0	0	0
<i>Cylichna diegensis</i>	1	0	0	0
Station PJ-6 [34°54.7'N, 120°49.9'W; 148 m]				
<i>Alvinia rosana</i>	248	42	17	59
<i>Balcis micans</i>	7	1	0	1
<i>Bittium fetellum</i>	1	0	0	0
<i>Epitonium</i>	5	0	0	0
<i>Eulima californica</i>	1	0	0	0
<i>Kurtzia arteaga</i>	1	0	0	0
<i>Turbonilla santarosana</i>	1	0	0	0
<i>Turbonilla</i> (Chemnitzia) sp. A	1	0	0	0
<i>Turbonilla</i> (Chemnitzia) sp. F	1	0	0	0
<i>Cylichna diegensis</i>	1	0	0	0

APPENDIX

Continued.

Locality and species	<i>n</i>	Major repairs	Minor repairs	Total repairs
<i>Cylichnella culcitella</i>	1	0	0	0
<i>Diaphana californica</i>	1	0	0	0
<i>Cadulus fusiformis</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	14	4	1	5
Station PJ-7 [34°55.8'N, 120°48.6'W; 123 m]				
<i>Alvinia rosana</i>	5	1	0	1
<i>Balcis micans</i>	1	0	0	0
<i>Balcis rutila</i>	1	0	0	0
<i>Eulima californica</i>	1	0	0	0
<i>Kurtziella beta</i>	3	0	0	0
<i>Mitrella tuberosa</i> (Carpenter, 1865)	3	0	1	1
<i>Cylichna diegensis</i>	2	0	0	0
<i>Siphonodentalium quadrifissatum</i>	21	1	0	1
Station PJ-8 [34°56.9'N, 120°49.9'W; 142 m]				
<i>Admete rhyssa</i>	1	0	0	0
<i>Alvinia rosana</i>	76	18	6	24
<i>Balcis micans</i>	4	0	0	0
<i>Balcis rutila</i>	4	0	1	1
<i>Epitonium</i>	1	0	0	0
<i>Kurtzia arteaga</i>	2	0	0	0
<i>Kurtziella beta</i>	2	0	0	0
<i>Odostomia phanella</i>	1	0	0	0
<i>Turbonilla santarosana</i>	1	0	0	0
<i>Cylichna diegensis</i>	3	1	0	1
<i>Siphonodentalium quadrifissatum</i>	12	2	0	2
Station PJ-9 [34°55.8'N, 120°51.2'W; 169 m]				
<i>Alvinia rosana</i>	28	2	1	3
<i>Balcis micans</i>	3	0	0	0
<i>Balcis rutila</i>	5	1	0	1
<i>Bittium fetellum</i>	3	0	0	0
<i>Epitonium</i>	2	0	0	0
<i>Kurtzia arteaga</i>	3	0	0	0
<i>Odostomia jewetti</i>	3	1	0	1
<i>Odostomia phanella</i>	95	4	5	9
<i>Odostomia pratoma</i>	1	0	0	0
<i>Turbonilla raymondi</i>	2	1	0	1
<i>Turbonilla santarosana</i>	2	0	0	0
<i>Turbonilla</i> (Chemnitzia) sp. A	2	0	0	0
<i>Cylichna diegensis</i>	1	0	0	0
<i>Cylichnella</i>	2	0	0	0
<i>Cylichnella culcitella</i>	10	0	0	0
<i>Rictaxis punctocaelatus</i> (Carpenter, 1864)	1	0	0	0
<i>Volvulella cylindrica</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	2	1	0	1
<i>Dentalium rectius</i>	11	3	0	3
Station PJ-10 [34°53.6'N, 120°49.9'W; 147 m]				
<i>Alvinia rosana</i>	218	29	10	39
<i>Balcis micans</i>	2	0	0	0
<i>Balcis rutila</i>	5	0	0	0
<i>Bittium fetellum</i>	3	0	0	0
<i>Epitonium</i>	1	0	0	0
<i>Kurtzia arteaga</i>	2	1	0	1
<i>Sabinella bakeri</i> (Bartsch, 1917)	1	1	0	1
<i>Turbonilla</i>	1	0	1	1
<i>Turbonilla painei</i> Dall & Bartsch, 1909	1	0	0	0

APPENDIX

Continued.

Locality and species	<i>n</i>	Major repairs	Minor repairs	Total repairs
<i>Turbonilla santarosana</i>	1	0	0	0
<i>Turbonilla</i> (<i>Chemnitzia</i>) sp. F	3	1	0	1
<i>Cylichna diegensis</i>	1	0	0	0
<i>Cylichnella culcitella</i>	2	0	0	0
<i>Siphonodentalium quadrifissatum</i>	12	3	0	3
Station PJ-11 [34°58.0'N, 120°49.9'W; 136 m]				
<i>Alvinia rosana</i>	172	42	6	48
<i>Balcis micans</i>	6	0	0	0
<i>Kurtzia beta</i>	2	0	0	0
<i>Odostomia dinella</i>	3	0	0	0
<i>Volvulella panamica</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	20	1	1	2
Station PJ-12 [34°55.6'N, 120°49.9'W; 145 m]				
<i>Alvinia rosana</i>	32	5	3	8
<i>Balcis micans</i>	3	0	0	0
<i>Bittium fetellum</i>	1	1	0	1
<i>Kurtziella beta</i>	1	0	1	1
<i>Odostomia</i>	2	1	0	1
<i>Odostomia dinella</i>	2	0	1	1
<i>Dentalium rectius</i>	1	0	0	0
Station PJ-13 [34°56.0'N, 120°49.9'W; 144 m]				
<i>Alvinia rosana</i>	46	7	3	10
<i>Balcis micans</i>	2	0	0	0
<i>Kurtzia arteaga</i>	1	0	0	0
<i>Kurtziella beta</i>	1	0	1	1
<i>Turbonilla raymondi</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	3	1	0	1
Station PJ-14 [34°55.8'N, 120°49.3'W; 134 m]				
<i>Alvinia rosana</i>	19	4	1	5
<i>Balcis micans</i>	2	0	0	0
<i>Balcis rutila</i>	1	0	1	1
<i>Kurtziella beta</i>	1	1	0	1
<i>Siphonodentalium quadrifissatum</i>	6	1	0	1
Station PJ-15 [34°55.8'N, 120°50.6'W; 155 m]				
<i>Alvinia rosana</i>	514	90	38	128
<i>Balcis micans</i>	2	0	0	0
<i>Odostomia dinella</i>	5	0	0	0
<i>Odostomia phanella</i>	1	0	1	1
<i>Turbonilla</i>	2	1	0	1
<i>Cylichnella culcitella</i>	2	0	0	0
<i>Siphonodentalium quadrifissatum</i>	3	1	0	1
Station PJ-16 [34°55.0'N, 120°49.0'W; 130 m]				
<i>Alvinia rosana</i>	24	4	0	4
<i>Balcis micans</i>	3	0	0	0
<i>Kurtziella beta</i>	2	0	0	0
<i>Siphonodentalium quadrifissatum</i>	7	1	0	1
Station PJ-17 [34°56.6'N, 120°49.0'W; 126 m]				
<i>Alvinia rosana</i>	45	8	2	10
<i>Epitonium</i>	1	0	0	0
<i>Odostomia dinella</i>	2	0	0	0
<i>Odostomia phanella</i>	1	0	0	0

APPENDIX

Continued.

Locality and species	<i>n</i>	Major repairs	Minor repairs	Total repairs
Station PJ-18 [34°56.6'N, 120°50.8'W; 158 m]				
<i>Alvinia rosana</i>	164	18	12	30
<i>Balcis rutila</i>	1	0	0	0
<i>Bittium fetellum</i>	2	0	0	0
<i>Odostomia dinella</i>	4	0	0	0
<i>Odostomia phanella</i>	1	0	0	0
<i>Cylichnella culcitella</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	1	1	0	1
<i>Dentalium rectius</i>	1	0	0	0
Station PJ-19 [34°55.0'N, 120°50.8'W; 167 m]				
<i>Alvinia rosana</i>	42	5	3	8
<i>Balcis micans</i>	2	0	0	0
<i>Balcis rutila</i>	2	0	0	0
<i>Kurtziella beta</i>	2	1	0	1
<i>Odostomia dinella</i>	4	0	0	0
<i>Odostomia phanella</i>	1	1	0	1
<i>Odostomia pratoma</i>	2	0	0	0
<i>Turbonilla santarosana</i>	4	0	0	0
<i>Cylichnella harpa</i>	2	0	0	0
<i>Dentalium rectius</i>	3	2	0	2
Station PJ-20 [34°50.4'N, 120°49.9'W; 148 m]				
<i>Alvinia rosana</i>	7	2	0	2
<i>Balcis micans</i>	4	0	0	0
<i>Epitonium</i>	1	0	0	0
<i>Kurtzia arteaga</i>	1	0	0	0
<i>Odostomia dinella</i>	1	0	0	0
<i>Turbonilla santarosana</i>	1	0	0	0
<i>Turbonilla (Chemnitzia) sp. F</i>	9	2	0	2
<i>Cylichnella culcitella</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	7	0	2	2
Station PJ-21 [35°01.2'N, 120°51.2'W; 143 m]				
<i>Alvinia rosana</i>	58	6	2	8
<i>Balcis micans</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	2	0	0	0
Station PJ-22 [34°55.2'N, 120°49.9'W; 143 m]				
<i>Alvinia rosana</i>	66	12	4	16
<i>Balcis micans</i>	4	0	0	0
<i>Kurtziella beta</i>	1	0	0	0
<i>Turbonilla (Chemnitzia) sp. F</i>	1	0	0	0
<i>Cylichna diegensis</i>	1	0	0	0
<i>Cylichnella</i>	2	1	0	1
<i>Cylichnella culcitella</i>	1	0	0	0
<i>Diaphana californica</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	11	1	0	1
Station PJ-23 [34°56.3'N, 120°49.9'W; 143 m]				
<i>Alvinia rosana</i>	119	30	6	36
<i>Balcis micans</i>	10	2	0	2
<i>Kurtzia arteaga</i>	1	0	0	0
<i>Kurtziella beta</i>	3	0	0	0
<i>Cylichna diegensis</i>	1	0	0	0
<i>Cylichnella culcitella</i>	2	0	0	0
<i>Diaphana californica</i>	1	0	0	0
<i>Volvulella panamica</i>	1	0	0	0
<i>Siphonodentalium quadrifissatum</i>	12	1	1	2

Observations on the Biology of *Turritella gonostoma* Valenciennes (Prosobranchia: Turritellidae) from the Gulf of California

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Abstract. *Turritella gonostoma* Valenciennes, 1832, is common in several areas in the northern Gulf of California, particularly during the winter months. It may move into shallow water at these times, perhaps following cool, nutrient-rich waters associated with seasonal upwelling, and move off into deeper water when water temperatures rise during the summer. It lays eggs in shallow water in February–April. Eggs hatch as veligers that swim in the plankton for 2–3 weeks. Preliminary feeding experiments suggest that this species does suspension feed, but not at a very high rate compared to other suspension-feeding mollusks. Analysis of oxygen isotopic variation in the shells of three individuals suggests that growth rates are high but variable, and that longevity is around two years.

INTRODUCTION

Turritelline gastropods (family Turritellidae, subfamilies Turritellinae and Protominae; MARWICK, 1957) are diverse and abundant components of many fossil and living marine benthic communities, and turritelline-dominated assemblages are common in the geological record; yet very little is known about the biology of individual species (see ALLMON, 1988, for review). Here we present new information on a single living species, *Turritella gonostoma* Valenciennes, 1832, from the Gulf of California (expanding and adding to an earlier summary; ALLMON, 1988), and put this information into the wider context of what is known about other turritelline species. Improved knowledge of the biology of these organisms may contribute to improved understanding of the mode of origin and environmental significance of turritelline-dominated fossil as-

semblages. Voucher specimens have been deposited in the Los Angeles County Museum of Natural History and the U.S. National Museum of Natural History.

GEOGRAPHIC DISTRIBUTION AND THERMAL RANGE

Turritella gonostoma occurs throughout the Gulf of California as far north as Bahia la Cholla, north of the town of Puerto Peñasco (31°20'N) (Figure 1) and as far south as the southwestern coast of Colombia (2°20'N); it has not been reported from the west coast of Baja California (records from the literature and collections of the Department of Malacology, Los Angeles County Museum). It is one of the most common turritelline species in the gulf, particularly in the north. In this region it occurs in shallow waters (<5 m) in variable densities (<1–100/m²), higher

values always being observed between December and May (ALLMON, 1988). The location of individuals during the remainder of the year remains unknown. Although PARKER (1964:98) reported large numbers of turritelline shells freshly deposited on beaches in the gulf, he did not collect a single live individual in extensive grab-sampling of benthic macrofauna.

At Bahia la Cholla, where most of our observations were made, average monthly water temperatures range from 13.8°C in January to 29.4°C in August (THOMSON, 1987, cited in FURSICH & FLESSA, 1987). RODEN & GROVES (1959) reported average surface water temperatures at Puerto Peñasco of 14.9°C in January and 31.2°C in August.

PARKER (1964:39) pointed out that the south side of Tiburon Island in the northern Gulf of California is the extreme northern end of the geographic range of many benthic invertebrate species, and suggested that one reason might be the extreme seasonal fluctuations in surface water temperature that characterize the northern gulf. Occasional winter cold snaps, during which water temperatures may fall to as low as 8°C, sometimes result in massive mortality of stenothermal algae and macroinvertebrates (FLESSA & EKDALE, 1987).

Whether individual turritelline species, or individual animals, are actually adapted to survive and reproduce in a wide range of temperatures is not known. It is possible, however, that at least some species are adapted to thermal instability in another way. If, as discussed by ALLMON (1988), at least some turritelline species are capable of moving significant distances, perhaps on the order of 10^2 – 10^3 m in days or weeks, this might allow them to move into shallow water, possibly to reproduce, during times of upwelling and cooler waters, and to move back out to deeper water afterward.

SUBSTRATE, LIFE POSITION, AND MOVEMENT

Individuals of *Turritella gonostoma* at Bahia la Cholla, Sonora, and Mulege, Baja California Sur occur both on and within fine to coarse sands in 0.5–2 m of water at low tide (VAUGHAN, 1983; ALLMON, 1988; HERTZ, 1990) (Figure 2). Some individuals we observed at Bahia la Cholla had their anterior end partly to completely buried (Figure 2A), the location of the aperture marked only by one or a pair of small, subcircular holes in the sand about 1 cm across. Others had only their apex buried, at a very low angle, in the sediment (Figure 2B), and still others were not covered by sand at all. The shell aperture was oriented perpendicular to the substrate surface in all stationary live individuals observed in their natural setting, both buried and exposed. Crawling individuals were oriented aperture down. Animals kept in laboratory aquaria assume similar orientations (ALLMON, 1988). Several species of macrophytic algae were growing on the apertural (left) side of the shell in a number of live individuals at Bahia la Cholla

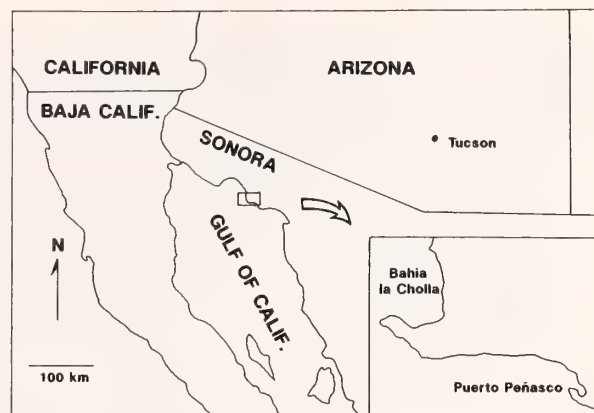


Figure 1

Map of the northern Gulf of California, showing location of Bahia la Cholla.

(Figure 2C, D), suggesting that these surfaces had been exposed above the sediment for some length of time. BUCHANAN (1958) and BATHAM (1969) also reported macrophytes on the shells of living turritellines. On one occasion we observed a single living individual buried vertically in the substrate, apex down (Figure 2E). Neither the significance of this orientation nor the means by which it is attained is known.

Although active burrowing was observed by individuals in aquaria, some burial in nature seems to be passive by tidal currents washing sediment over the shell. In aquaria, individuals usually remained motionless, partly or wholly buried in the sediment, but on occasion we observed much greater levels of activity. Animals as large as 10 cm in length are able to pull themselves out of the water and crawl up the sides of aquaria. Activity seemed to be greatest at night.

SUSCEPTIBILITY TO PREDATION

Observed rates of predation on *Turritella gonostoma* by drilling gastropods is above average for Recent turritellines (DUDLEY & VERMEIJ, 1978; see also ALLMON *et al.*, 1990). We have observed predation on *T. gonostoma* in the laboratory by *Muricanthus nigrinus* Philippi, 1845, which also lives in the Gulf of California. The following description of an encounter between these two species is representative of several we observed. At approximately 0900 hr on 23 April 1990, one *M. nigrinus* attached itself to a *T. gonostoma* that was resting completely exposed on the substrate. The turritellid gave no observable reaction. At approximately 1600 hr on 30 April the turritellid became agitated, as indicated by an extrusion of mucus and movement of its cephalopodal mass erratically about the aperture; we presume that the predator had penetrated its shell at this time. When the *Muricanthus* was removed, we observed that only the visceral mass, and not the cephalopodal mass, had been consumed.



Figure 2

Orientations of live *Turritella gonostoma* at Bahia la Cholla. A. Specimen with only posterior (apical) end buried in sediment. Depth ≈ 1 m at low tide. B. Specimen with only anterior (apertural) end buried in sediment. Depression (arrow) marks location of aperture and incurrent and excurrent siphons. Depth ≈ 1 m at low tide. In both A and B, apertures are oriented normal to the sediment surface. C and D. Specimens with macrophytic algae growing on shell. C taken in life position at depth ≈ 1 m at low tide. D taken in aquarium in the field; specimen pictured with egg mass found next to it in about 1-m depth at low tide. E. Live specimen oriented apex down, exposed on tidal flat at low tide.

FEEDING

Limited circumstantial evidence and direct observations of other species indicate that at least some, and perhaps most, living turritellines are predominantly suspension feeders (*e.g.*, YONGE, 1946; ALLMON, 1988). Turritellines suspension feed by taking water in through an inhalant siphon, trapping particles on the ctenidial surfaces, and transporting them to the mouth in a mucous rope (YONGE, 1946; FRETTER & GRAHAM, 1962:571). Water is expelled from an excurrent siphon formed by a fold of mantle tissue. When approximately 1 mL of fluorescein dye was introduced into the inhalant siphon of an individual of *Turritella gonostoma*, it began to be expelled by a smooth laminar flow in approximately 10–12 sec, a relatively rapid rate compared to other gastropods and suggestive of strong water-pumping ability (R. Linsley, personal communication).

Other data, however, suggest that at least some turritellines may feed by other means (*e.g.*, deposit feeding or surface grazing) at least part of the time (ALLMON, 1988). There evidently have been no measurements of either rates of suspension feeding or the degree to which suspension feeding is obligate in any turritelline species. We therefore undertook simple measurements of filtration rates by *Turritella gonostoma*.

Methods

Three snails were placed in individual glass bowls containing a suspension of the naked flagellated alga *Isochrysis galbana* at concentrations of about 16×10^4 cells/mL. Animals were kept in light or dark conditions at 19–20°C. Algal concentrations were measured hourly using a model ZM electronic particle counter (Coulter Electronics). Filtration rates were calculated using the method described in NEWELL (1979:463). Individuals were removed from their shell, rinsed with distilled water, dried at 40°C for 12 hr, and weighed to determine tissue weight.

Results

Two trials were run with each animal under both light and dark conditions. The highest filtration rates observed are plotted in Figure 3 and summarized in Table 1. In four of the 12 trials, particle concentrations increased, indicating that no net particle clearance was taking place and, probably, that pseudofeces were being produced. Results differed by individual animal; the largest (individual No. 2) showed consistently high filtration rates, while individual No. 1 never showed any measurable particle clearance. Filtration rates appeared to be higher in the dark than the light, but the sample size is too small to confirm this pattern.

Even the highest filtration rates observed in these turritellids are 1–2 orders of magnitude lower than those commonly observed in other active filter feeders (*e.g.*, *Crepidula fornicata* by NEWELL & KOFOED, 1977; many bi-

Table 1

Maximum observed filtration rates of three individuals of *Turritella gonostoma* in laboratory feeding experiments.

Animal	Observed shell length (mm)	Dry tissue mass (g)	Duration of feeding (hr)	Avg. filtration rate (mL/hr/g) [no. of trials]
1	90.35	0.26	18.0 (light) 5.0 (dark)	0.00 [2] 0.00 [2]
2	102.10	0.45	3.0 (light) 7.0 (dark)	1.98 [2] 2.94 [2]
3	80.25	0.12	5.0 (light) 8.0 (dark)	0.00 [2] 5.08 [2]

valves, see NEWELL, 1979). At least two explanations are possible for these very preliminary results. The animals may not have exhibited their normal feeding behavior in the laboratory setting; although they appeared healthy, they may not have been. Alternatively (or in addition), these turritellines may be very minimal suspension feeders, either because of low metabolic needs or because they obtain food in other ways (*e.g.*, grazing and/or deposit feeding).

REPRODUCTION

Data from a number of living turritelline species suggest that reproduction is seasonal (ALLMON, 1988). All available anecdotal reports of the occurrence of eggs of *Turritella gonostoma* in the northern half of the Gulf of California indicate that spawning occurs only in the late winter and early spring (February–April; ALLMON, 1988; HERTZ, 1990). Large, apparently adult individuals are often found associated with egg masses, either individually or in large aggregations of hundreds to thousands (ALLMON, 1988; HERTZ, 1990; Figure 4).

Egg masses contain 200 to 300 egg capsules (Figure 2D), which are loosely attached to a central membrane and a simple holdfast, which may be secured to sandy or hard substrates. Egg capsules are 2–3 mm in diameter, and just before hatching contain 1–12 veligers (mean = 3.65, $n = 23$) (Figure 5).

We have observed egg laying in the field once. In April 1987 at Bahia la Cholla a female was observed oriented horizontally at low tide in a small tidal channel in 1–2 cm of water. She had already attached a holdfast at one end of the egg mass to the substrate (a shallowly buried, dead bivalve shell) when observations began. Eggs were extruded over the next 15–20 min in several, seemingly peristaltic surges. A holdfast at the other end of the egg mass was then attached to a nearby rock, the two attachment points being about 4 cm apart. This arrangement allowed the egg mass to form an arch, which moved back and forth with the waves. Following completion of egg laying, the

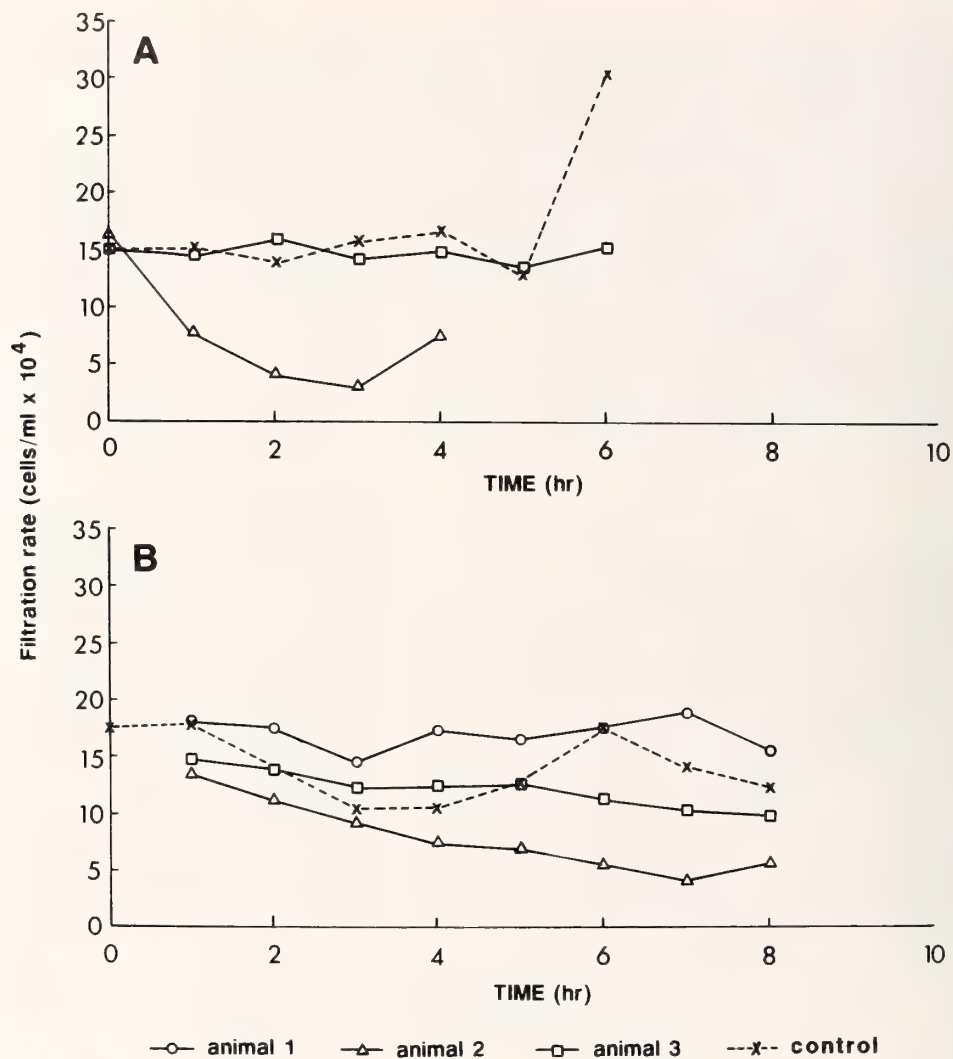


Figure 3

Filtration rates of three individuals of *Turritella gonostoma* in the laboratory. Graphs show highest observed filtration rates (data summarized in Table 1). A. Dark. B. Light. See text for details.

female remained at the site as long as observations continued, but was absent the following morning (approximately 12 hr later).

Fourteen days after being laid, a portion of the egg mass was transported to a laboratory, and eggs began to hatch en route. This may have been due to disturbance in transit, but is consistent with experience with other egg masses collected in the field and whose laying date was not known but which hatched after 14–21 days in laboratory aquaria.

From the egg capsules hatched veligers (Figure 6) that swam in laboratory aquaria for 10–12 days before settling and metamorphosing. The first veligers to settle appeared to prefer the glass sides of the aquaria. Veligers added at least one full whorl to the shell during their planktonic period; newly settled juveniles generally had around 2½

whorls (Figure 6; ALLMON, 1988). Eggs and veligers are very sensitive to high temperatures. In one mass left overnight at room temperature (22°C) all veligers died.

GROWTH

Life-span and age of reproduction have been determined by direct observation in only one turritelline species. In the Australian species *Gazameda gunnii* (Reeve, 1849), reproduction begins when the adults are 2.5–3 years of age, and is repeated throughout a life-span of 6–7 years (CARRICK, 1980). WRIGHT (1956) observed well-developed gonads in individuals of the northeastern Atlantic species *Turritella communis* Risso, 1826, as small as 23 mm in length. According to the growth curves calculated



Figure 4

Several live individuals of *Turritella gonostoma* (arrows) surrounded by abundant egg masses, exposed at low tide on the tidal flat at Bahía la Cholla. Photo taken in April 1987.

by CADÉE (1968), this corresponds to an age of less than one year. Life-span is unknown, but maximum reported size is approximately 45 mm, corresponding to an age of just over two years on Cadée's curve. Buchanan (personal communication) has attempted to age individuals of *T. communis* by counting collabral growth lines, and on this basis suggests a longevity of at least 15 years, with population modes of 10–11 years.

No such data have ever been presented for *Turritella gonostoma*. We have been unable to keep large numbers of healthy, feeding adults alive in the laboratory for more than about five months, and so have not made direct observations. The only direct observation of growth we have been able to make in *T. gonostoma* was provided by the repair of shell breakage by one individual: slight breakage around the aperture occurred during transport, and by the time the animal died two months later it had laid down approximately 5 mm of thin, translucent white shell around the outside of the aperture (Figure 7).

In the absence of other direct observations of growth, we sought to assess the growth history of *Turritella gonostoma* via analysis of stable isotope profiles of shell car-

bonate. Seasonal cycles in the oxygen and/or carbon isotope records ($^{18}\text{O}/^{16}\text{O}$, $^{13}\text{C}/^{12}\text{C}$) have been used to interpret the age and growth rate of many species of fossil and Recent mollusks (*e.g.*, KRANTZ *et al.*, 1987). This technique has found its widest application in work on marine bivalves, but growth histories of marine gastropods have also been reconstructed from stable isotope studies (*e.g.*, WEFER & KILLINGLEY, 1980).

Materials and Methods

Three specimens of *Turritella gonostoma* from Bahía la Cholla were used for isotopic study. These specimens had shell lengths of 109, 87, and 69 mm (these lengths will be used to identify the specimens in the discussion that follows). Specimens 87 and 69 were collected alive on 13 February 1987, while specimen 109, collected on the same day, was not alive. The shells of specimens 87 and 69 were complete, whereas the apical end of specimen 109 was abraded. By comparison with the complete shells, we estimate that the initial six whorls were missing from 109 (Table 2).



Figure 5

Egg capsule of *Turritella gonostoma* encrusted with sand grains. Scale = 1 mm.

The outer surface of each specimen was washed to remove extraneous materials. Using a small dental burr (diameter <0.5 mm) mounted in a hand-held drill, samples of aragonitic shell material, each weighing approximately 0.5 mg, were obtained by grinding shallow grooves into the outer shell layer of each whorl in an orientation parallel to the external growth lines (Figure 8). Detailed, serial sampling of specimen 109 yielded 117 separate samples, each spaced about 1–2 mm apart (Figures 8, 9a). After analyzing these samples isotopically and noting the smooth pattern of isotopic change throughout ontogeny, we decided

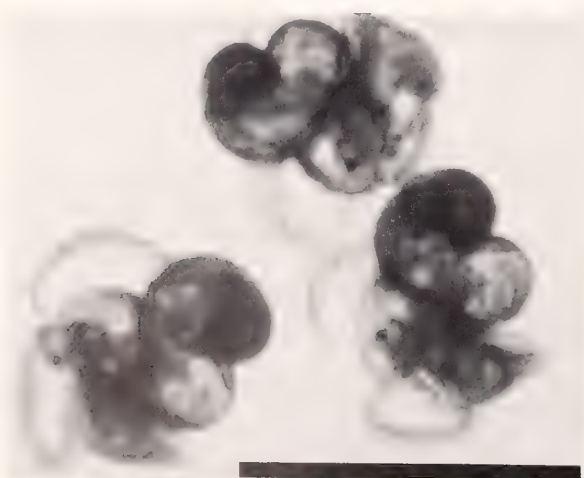


Figure 6

Veligers of *Turritella gonostoma* approximately 5 days after hatching. Scale bar = 1 mm.



Figure 7

Specimen of *Turritella gonostoma* in laboratory aquarium, showing regrowth of broken shell achieved in two months (arrow).

that such a dense sampling strategy was not required for the other two specimens. Only one sample per whorl was recovered from specimens 87 (Figure 9b) and 69 (Figure 9c), with the exception that because of small initial whorls in specimen 69, whorls 1 and 2 were combined to produce one sample, as were whorls 3 and 4. This resulted in 12 samples from the 14 whorls of specimen 69 (Figure 9c).

Each sample of powdered aragonite was washed in 15% H_2O_2 for 3 hr to remove organic contaminants. The H_2O_2 was then pipetted off and the samples were flushed with distilled H_2O , followed by two consecutive washings with methanol (99.9%). The samples were then dried overnight and stored. All samples were analyzed according to standard techniques (WILLIAMS *et al.*, 1977), which involved an initial reaction *in vacuo* with "100%" orthophosphoric acid at 70°C for 0.25 hr. An on-line, carbonate preparation system facilitated the production and purification of the evolved CO_2 gas. The isotopic difference between the derived sample CO_2 and the PDB standard was determined with a fully automated, VG Isogas PRISM Series I mass spectrometer equipped with triple collectors and micro-inlet system. All values are reported in the standard (δ) notation where:

$$\delta^{18}O = [(^{18}O/^{16}O)_{\text{sample}} / (^{18}O/^{16}O)_{\text{standard}} - 1] \times 10^3 \text{ per mil}$$

Determinations of $\delta^{13}C$ were made concurrently with $\delta^{18}O$. Average reproducibility, as evidenced by duplicate analyses and standards run before and after sample strings, was approximately ± 0.1 per mil (‰).

Results

The stable isotope records for each specimen are plotted in Figure 9 in standard fashion, with lighter (depleted) values toward the top. This graphical convention derives from paleotemperature interpretations of the isotopic variations ($\delta^{18}O$ in particular) in which warmer temperatures, and their correspondingly depleted isotopic values, are

Table 2
Specimens of *Turritella gonostoma* used in
isotopic age analysis.

Observed length (mm)	Estimated length (mm)	Observed no. of whorls	Estimated no. of whorls	Estimated age (years)
109	125	11	17	1.5
87	87	15	15	1.5
69	69	14	14	1.5

plotted toward the top, while cooler temperatures and heavier (enriched) values toward the bottom. All of these figures plot the record of isotopic change ontogenetically, from the shell apex (left) to the aperture (right).

The most detailed isotopic profiles were obtained for specimen 109. Sample spacing remained constant in this individual at 1–2 mm so that with ontogenetic whorl expansion, the number of samples recovered per whorl increased steadily toward the aperture. The 117 paired oxygen and carbon isotopic analyses exhibited a smooth pattern of variation throughout ontogeny, except for the final few samples (111–117) which indicated an episode of comparatively abrupt change.

The $\delta^{18}\text{O}$ record in specimen 109 is characterized by a strong cyclicity. Approximately 1.5 cycles are evident, with a maximum isotopic amplitude of 2.7 per mil (-2.0 to $+0.7$). The initial, broad cycle, which includes whorls 7 through the beginning of 17, differs sharply from the final one-half cycle, which occurs entirely within the latter half of whorl 17. This pattern almost certainly reflects an ontogenetic decline in shell growth rate (as discussed below). The carbon isotope record, in contrast, shows little or no cyclicity. Following a slight initial enrichment of about 0.5 per mil (from the apex to whorl 11), the remainder of the record reveals a weak ontogenetic trend toward lighter carbon isotopic values. This trend is gradual for the most part but, like the oxygen record, it is abrupt over the last half of the final whorl. The $\delta^{13}\text{C}$ values range between $+2.4$ and $+3.6$ per mil with a maximum amplitude of 1.2.

The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records for specimens 87 and 69 are broadly comparable to those observed for specimen 109. The record of specimen 87 (Figure 9b) begins with a protracted episode of nearly constant $\delta^{18}\text{O}$ values (whorls 1–11). An abrupt enrichment occurs in whorl 12, followed by depletion through whorl 14, completing the first major cycle. The slightly enriched value from the final whorl (15) suggests that a second cycle had begun at the time of capture. The $\delta^{18}\text{O}$ values range between -1.9 and -0.3 per mil for an overall isotopic amplitude of 1.6. In specimen 69 (Figure 9c) the $\delta^{18}\text{O}$ pattern is similar except that the enrichment phase of the cycle begins sooner (whorl 7–8) than in specimen 87 and is more gradual in nature. The $\delta^{18}\text{O}$ values range from -1.5 to $+0.5$ per mil for a slightly



Figure 8

Photograph of *Turritella gonostoma* specimen 109 showing serial isotopic sampling pattern. Specimen length = 109 mm.

greater amplitude of 2.0. As in specimen 87, the enriched $\delta^{18}\text{O}$ value from the final whorl of specimen 87 suggests a second cycle was initiated prior to capture.

As in specimen 109, the $\delta^{13}\text{C}$ profiles of specimens 87 and 69 do not reveal major cycles. The pattern in specimen 87 is one of gradual enrichment from whorl 1 through 13, followed by a brief episode of depletion across the final two whorls. The $\delta^{13}\text{C}$ values vary between $+1.9$ and $+3.1$ per mil (isotopic amplitude = 1.2). In specimen 69 the overall $\delta^{13}\text{C}$ amplitude is even smaller (0.4), with values ranging from $+2.4$ to $+2.8$ per mil, and no clear ontogenetic trends are evident throughout the record. Extremely weak correlations were observed between the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records of any particular specimens, as evidenced by r^2 values of 0.089, 0.032, and 0.035 for specimens 109, 87, and 69, respectively.

Discussion

The major cycles in the $\delta^{18}\text{O}$ profiles of all three specimens are best interpreted in terms of the annual cycle of temperature change in the northern Gulf of California.

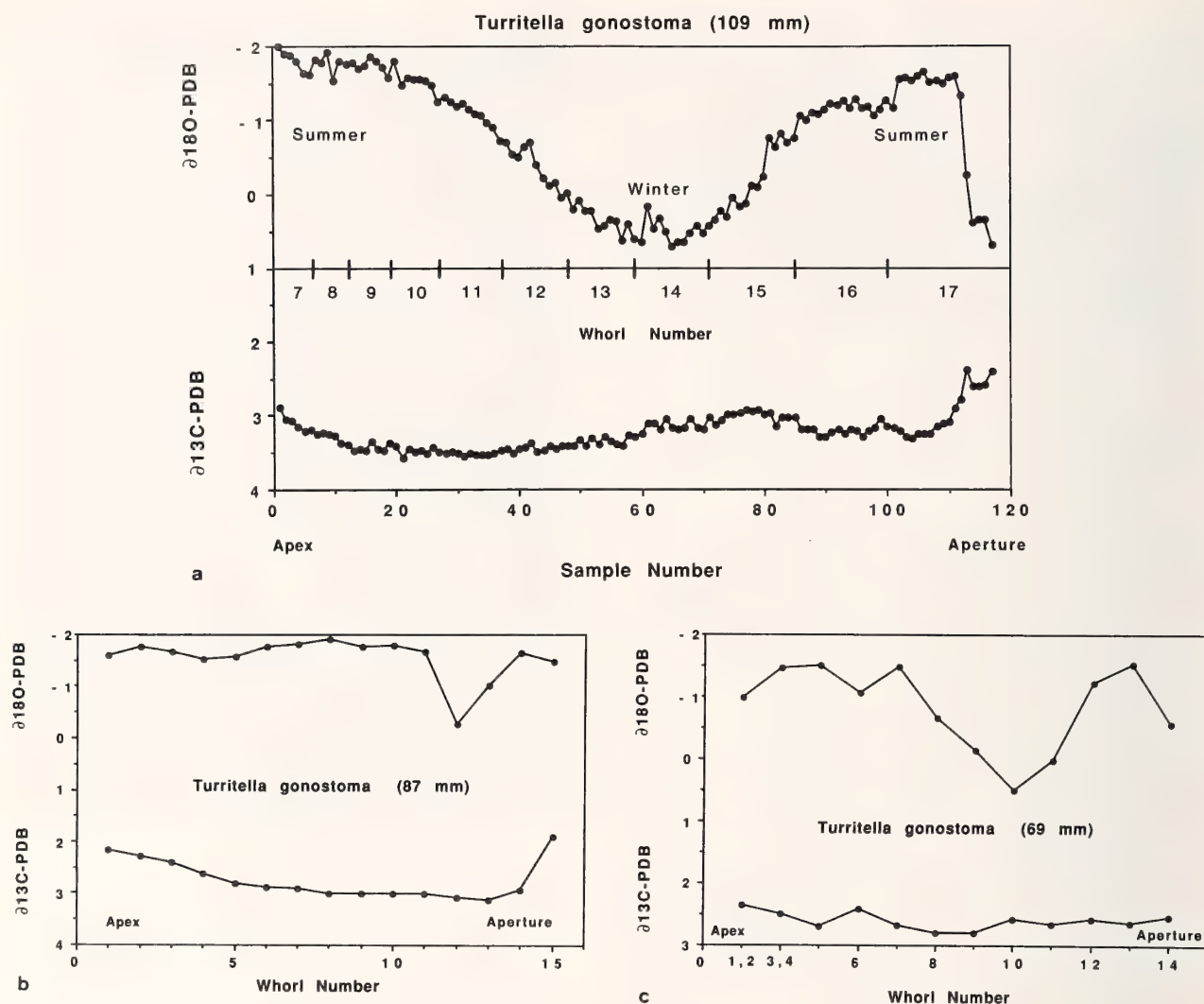


Figure 9

Plots of oxygen and carbon isotopic records, relative to the PDB standard, for three specimens of *Turritella gonostoma* from Bahia la Cholla. Results are plotted from the apex (left) to aperture (right). a. Specimen 109; 117 paired analyses are plotted in serial, ontogenetic order from left to right. b. Specimen 87; whorl numbers (= sample numbers) increase in ontogenetic order left to right. c. Specimen 69; whorl numbers (= sample numbers) increase in ontogenetic order left to right.

Mollusks typically form their shell at or near oxygen isotopic equilibrium with seawater and, barring significant salinity variations, the influence of temperature upon the $\delta^{18}\text{O}$ composition of shell carbonate is well constrained. Strong seasonality, such as obtains in the northern gulf, has been implicated as the principal cause of such cyclical variation in ontogenetic $\delta^{18}\text{O}$ profiles in a variety of mollusks (*e.g.*, ERLKENKEUSER & WEFER, 1981; WILLIAMS *et al.*, 1982; JONES, 1983; JONES *et al.*, 1983, 1989; KRANTZ *et al.*, 1984; CHINZEI *et al.*, 1987; ROMANEK *et al.*, 1987). Because the changes in $\delta^{18}\text{O}$ closely track the annual temperature cycle, it is possible to calculate the number of

years a specimen has lived and to approximate the range of temperatures over which shell formation has occurred.

The $\delta^{18}\text{O}$ record of specimen 109 (Figure 9a) represents the best data set of the three for isotopic calculations. As indicated, summer $\delta^{18}\text{O}$ values reach -2.0 per mil in this specimen while winter values extend to $+0.7$ per mil, for a total range of 2.7. According to the relationships describing equilibrium oxygen isotopic fractionation between calcium carbonate and water at environmental temperatures (summarized by ANDERSON & ARTHUR, 1983), a 1.0 per mil change in carbonate $\delta^{18}\text{O}$ corresponds to a change of about 4°C in temperature. Hence, the measured range

in $\delta^{18}\text{O}$ of 2.7 per mil suggests an annual range in seawater temperature of approximately 11°C.

Water samples were not collected as part of this study. Nevertheless, by making the reasonable assumption that the oxygen isotopic composition of the water in which specimen 109 grew approximated the modern global marine average, the aragonite-water fractionation relationship of GROSSMAN & KU (1986) provides a way to estimate the temperature regime under which calcification occurred. Substituting the end-member $\delta^{18}\text{O}$ values of -2.0 and +0.7 into this equation yields a maximum (summer) temperature of about 28°C and a minimum (winter) temperature of about 17°C. These estimates match actual measured temperatures from Bahia la Cholla remarkably well (see above).

Theoretically, the $\delta^{18}\text{O}$ records in specimens 87 and 69 would yield similar temperature estimates if the isotopic sampling scheme had been as detailed as that of specimen 109. The reduced annual isotopic amplitude measured in specimens 87 and 69 results from the coarse sampling pattern, which has the effect of homogenizing the seasonal oxygen isotopic signal and thereby minimizing the extent of the yearly variation.

Based on the number of yearly cycles in the $\delta^{18}\text{O}$ records of the three specimens of *Turritella gonostoma*, only specimen 109 was equal to or slightly older than about 1.5 years at the time of death (Table 2). Specimen 109 had experienced two summers and was beginning its second winter when it died (Figure 9a). Because of the coarser sampling scheme adopted for specimens 87 and 69, subdividing the yearly cycles into seasons was more difficult. Nevertheless, both individuals appear to have begun their second year of life when they were collected (Figures 9b, c). Neither lived longer than 1.5 years.

Using these interpretations of the $\delta^{18}\text{O}$ data, a growth curve for each specimen of *Turritella gonostoma* was constructed (Figure 10). Growth rates are clearly fastest in the first year of life, slowing significantly thereafter. In fact, the samples from the apertural end of specimen 109 (Figure 9a) suggest that the decline in growth rate may be rather dramatic during the second year of life. The most rapid seasonal growth seems to occur during the summer, particularly during the first year. This is suggested by the numerous depleted $\delta^{18}\text{O}$ values at the beginning of each profile that represent the early shell whorls and record "warm" temperatures. Although the initial six whorls of specimen 109 are missing, their small size and rapid growth rate (based on comparison with the other two specimens) suggest that this animal initiated growth in either late spring or early summer. This is consistent with the observed timing of reproduction in *T. gonostoma* from the northern Gulf of California, discussed above.

Although it is possible that these individuals lived for some unknown length of time without significant shell growth, straightforward interpretation of the data suggests that this species is not long-lived. In its estimated total

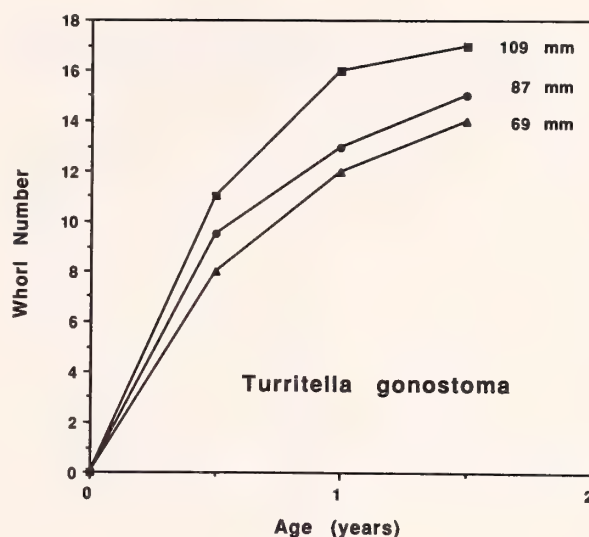


Figure 10

Growth curves (whorl number vs. age) for *Turritella gonostoma* specimens 109, 87, and 69, based on interpretations of annual cycles in $\delta^{18}\text{O}$ records (see Figure 9).

length (Table 2) specimen 109 exceeds reported average adult sizes for *Turritella gonostoma* (100 mm—ABBOTT & DANCE, 1982; 115 mm—KEEN, 1971). The comparatively young age (<2 years), as well as the dramatic growth rate reduction seen in the last whorl of this large specimen, favor an interpretation of short life-span (2 years or less) for this species. Even if the animals tracked cooler waters to some degree by moving into greater depths in the summer (see below), the strong cyclicity in the isotopic signal virtually demands a short life-span in these specimens.

Because the smaller specimens (87 and 69) are approximately the same age as 109, the larger size of the latter must have resulted from higher growth rate. This pattern of large specimens growing faster (as opposed to living longer) than their smaller counterparts has been observed in a variety of bivalves (*e.g.*, JONES, 1980; JONES *et al.*, 1989), and may hold equally well for gastropods.

In a study of strombid gastropods from Bermuda, WEFER & KILLINGLEY (1980) also related cycles in $\delta^{18}\text{O}$ profiles directly to seasonal temperature variation. The $\delta^{13}\text{C}$ records, in contrast, proved much more difficult to interpret, despite exhibiting a fair degree of cyclicity. Two major factors contribute to this situation: (1) carbon isotopic composition of carbonate skeletons has received less study than the interpretation of oxygen isotopic ratios (WEFER & KILLINGLEY, 1980), and (2) whereas temperature can often be isolated as the principal cause of oxygen isotopic variation, no such simple cause has been identified for carbon. Possible influences on the $\delta^{13}\text{C}$ composition of molluscan shell carbonate include: variations in ambient total dissolved carbon (TDC) resulting from changes in

productivity, runoff, upwelling, mixing, or other factors (e.g., EISMA *et al.*, 1976; KILLINGLEY & BERGER, 1979; ARTHUR *et al.*, 1983); temperature (GROSSMAN & KU, 1986); mixing of metabolic carbon derived from various food sources with dissolved inorganic carbon (TANAKA *et al.*, 1986); fractionation due to changes in shell growth rate (i.e., CaCO_3 precipitation rate; TURNER, 1982); and/or organismal vital effects of various kinds (ROMANEK & GROSSMAN, 1989).

The $\delta^{13}\text{C}$ profiles of the three turritelline specimens analyzed here (Figure 9) display much less variation than the strombids from Bermuda. If, as suggested by ALLMON (1988), turritellines in the Gulf of California occur in large numbers in areas of seasonal upwelling, it is possible that *Turritella gonostoma* at Bahia la Cholla moves into shallow water in the winter coincident with upwelling and moves offshore into deeper water during the summer. Following cooler, nutrient-rich water might have the effect of damping the ^{13}C signal in the shell (e.g., KILLINGLEY & BERGER, 1979; ARTHUR *et al.*, 1983). Only more detailed work can confirm this possibility.

CONCLUSIONS

Although the results presented here are preliminary and based on small sample sizes, they have implications for the interpretation of turritelline paleobiology and the ecology and taphonomy of turritelline-dominated fossil assemblages.

(1) Age and shell size appear to have no direct relationship to one another in *Turritella gonostoma*. If this applies to other turritellines as well, paleontological studies of heterochrony (which usually use size as a proxy for age) will be limited to conclusions about pattern (i.e., peramorphosis vs. paedomorphosis) rather than process (e.g., progenesis vs. neoteny) (see JONES, 1988, for further discussion).

(2) These gastropods are surprisingly young for their size. If the interpretation of short life-span is correct for these and other turritellines, it suggests that growth rates are very high. If all or most individuals of a species in an aggregation are of the same age, this implies that turritellines may be opportunistic, "boom-and-bust" species (e.g., LEVINTON, 1970).

(3) Patterns of density in turritelline-dominated assemblages, Recent or fossil, may be due less to patterns of recruitment (as in many other benthic invertebrates; e.g., BUTMAN, 1987) than to patterns of seasonal movement, migration, and/or aggregation.

A great deal of further investigation is needed to test and expand upon the conclusions presented here.

(1) We still do not know when, why, and to what degree turritellines burrow.

(2) While it is known that at least some turritellines feed by methods other than suspension feeding (see ALLMON, 1988), it remains to be determined to what degree this is the case in different species.

(3) Many more data are needed on the interaction between turritellines and their predators. Can they escape? If so, how do they and how often?

(4) Are all turritellines as short-lived as *Turritella gonostoma* appears to be?

Investigation into these topics will greatly increase our understanding of the history and biology of this important group of gastropods.

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Simulathena papuensis, a New Planaxid Genus and Species from the Indo-West Pacific

by

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Abstract. *Simulathena papuensis*, sp. nov., is monotypic, has a plain, thin littorinid-like shell with a large aperture and wide shallow anterior canal, and is sculptured with weak spiral incised lines. The periostracum is moderately thick and the lenticular operculum with terminal nucleus is typical of planaxids. The taenioglossate radula is very similar to those of three planaxid genera and also resembles that of *Fossarus*. A large, extensive subhemocoelic brood pouch of ectodermal origin fills the headfoot, extending anteriorly into the head. A pair of mantle papillae extends from the exhalant siphon. The osphradium is widely separated from the broad, shallow ctenidium. Brooded embryos with large shells hatch from the brood pouch as juvenile snails. *Simulathena* is the sister group of the *Hinea*, *Holcostoma*, *Supplanaxis* clade, which also includes the Fossarinae.

INTRODUCTION

Study of an unidentified, marine intertidal prosobranch from Yule Island, Papua New Guinea, has revealed a new genus and species of the planaxid group. The family Planaxidae Gray, 1850, a relatively small group of taxa, was reviewed by HOUBRICK (1987) and was thought to comprise six genera and about 20 species throughout the world. HOUBRICK (1990) subsequently allocated *Fossarus* Philippi, 1841, under the subfamily Fossarinae Troschel, 1861, to the Planaxidae, thereby expanding the family. It is therefore surprising to discover yet another genus and species to add to the family. The new taxon, lacking the thick shell characteristic of so many other planaxid taxa, has a generalized littorinid shell shape and a squat, rather smooth and thin shell. Radular, opercular, and anatomical investigations indicate that the new taxon shares a number of features with other planaxid taxa. A description and discussion follow.

MATERIALS AND METHODS

The examined specimens came from the Kanudi Marine Laboratory and were sent by the Papua New Guinea Department of Fisheries to the Australian Museum, Sydney, for identification. Five preserved specimens, which constitute the type lot, were studied and two of these dissected under a Wild M-5 dissecting microscope for anatomical study. One of the specimens was broken and was

not used for shell measurements. Although preservation was not optimal, sufficient anatomical features were available for rudimentary character analysis and a description of gross anatomy. However, several important systems, in particular the pallial oviducts, could not be described. Embryonic shells and the radula were studied using a Hitachi S-570 scanning electron microscope.

RESULTS

Simulathena Houbrick, gen. nov.

Diagnosis: Shell thin, squat, having inflated whorls sculptured with weak spirally incised lines, large, fat body whorl, smooth outer lip and very weak, shallow anterior canal. Operculum lenticular with subterminal nucleus. Radula having triangular rachidian tooth with pair of cusps high on basal plate, beneath cutting edge cusps, and lateral tooth with very wide, long lateral extensions of basal plate. Pair of mantle tentacles emerge from exhalant siphon. Large subhemocoelic cephalic brood pouch containing embryos having direct development, emerging as small snails.

Etymology: “like Athena,” a Latin combination of *simul*, meaning “like,” and Athena, the Greek goddess who sprang forth from the head of Zeus, in reference to direct development in the cephalic brood pouch.

Remarks: This genus appears to be monotypic and differs from other planaxid genera in having a light, thin shell.

The pair of mantle tentacles emerging from the exhalant siphon is distinctive and does not occur in other members of the family. The large embryos and extensive brood pouch extending forward into the head are also unusual.

It is unfortunate that only four specimens were available for study and that their anatomy is only partially known, but it is clear from what has been examined that this species represents an undescribed genus.

Simulathena papuensis Houbrick, sp. nov.
(Figures 1–13)

Description: *Shell* (Figures 1–3, Table 1): The shell is thin, squat, and globose, comprising about five inflated whorls weakly sculptured with incised spiral lines. The protoconch and embryonic whorls (Figures 4–6) are unsculptured, having a smooth gradual transition into the incised spiral lines of the adult shell. The adult whorls, exclusive of the body whorl, each have 4 spiral incised lines and numerous microscopic and weak axial striae. The suture is distinct and slightly sunken into each successive whorl. The body whorl is very large, comprising over 75% of the shell length and is sculptured with about 14 spiral incised lines. The aperture is ovate and large, nearly two-thirds the shell length, and has a concave columella with a weak callus and a smooth edged, rounded outer lip, slightly pointed at the shell base. The anterior canal is merely a slight shallow depression in the basal part of the peristome adjacent to the columella. A well-developed, tan-to-olive colored periostracum covers the shell, and also occurs on embryonic shells. Under the periostracum, the shell is white with 3 broad light-brown spiral bands.

The operculum (Figures 7, 8) is corneous, brown, and lenticular, having a terminal nucleus and many growth lines. The attachment scar is elongate and narrow (Figure 8).

Anatomy: The animal (Figure 9) is tightly coiled, having a very large body whorl, which comprises the mantle cavity, the pericardial cavity, and part of the kidney. The visceral whorls comprise the large stomach, digestive gland, and gonad. The headfoot is large and muscular with a broad snout (Figure 9, sn), which is enlarged and bilobed at the tip and has short cephalic tentacles, each with a small black eye on the outer side of the tentacular base. A conspicuous birth pore (Figure 9, bp) lies in the right side of the neck in females. The thick columellar muscle (Figure 9, cm) is short but broad, enveloping the ventral side of the body whorl. The large muscular foot is broad and thick, and has a long anterior mucus gland. The mantle skirt is wide and its ventral and dorsal edges are smooth, except for some small papillae (Figure 9, mp) at the inhalant siphon (Figure 9, inh). Emerging from the exhalant siphon are two enlarged, tentaculate papillae (Figure 9, exp) attached to the inner surface of the mantle skirt. The

Table 1

Shell measurements (mm) and meristics of the holotype (*) and three paratypes of *Simulathena papuensis*.

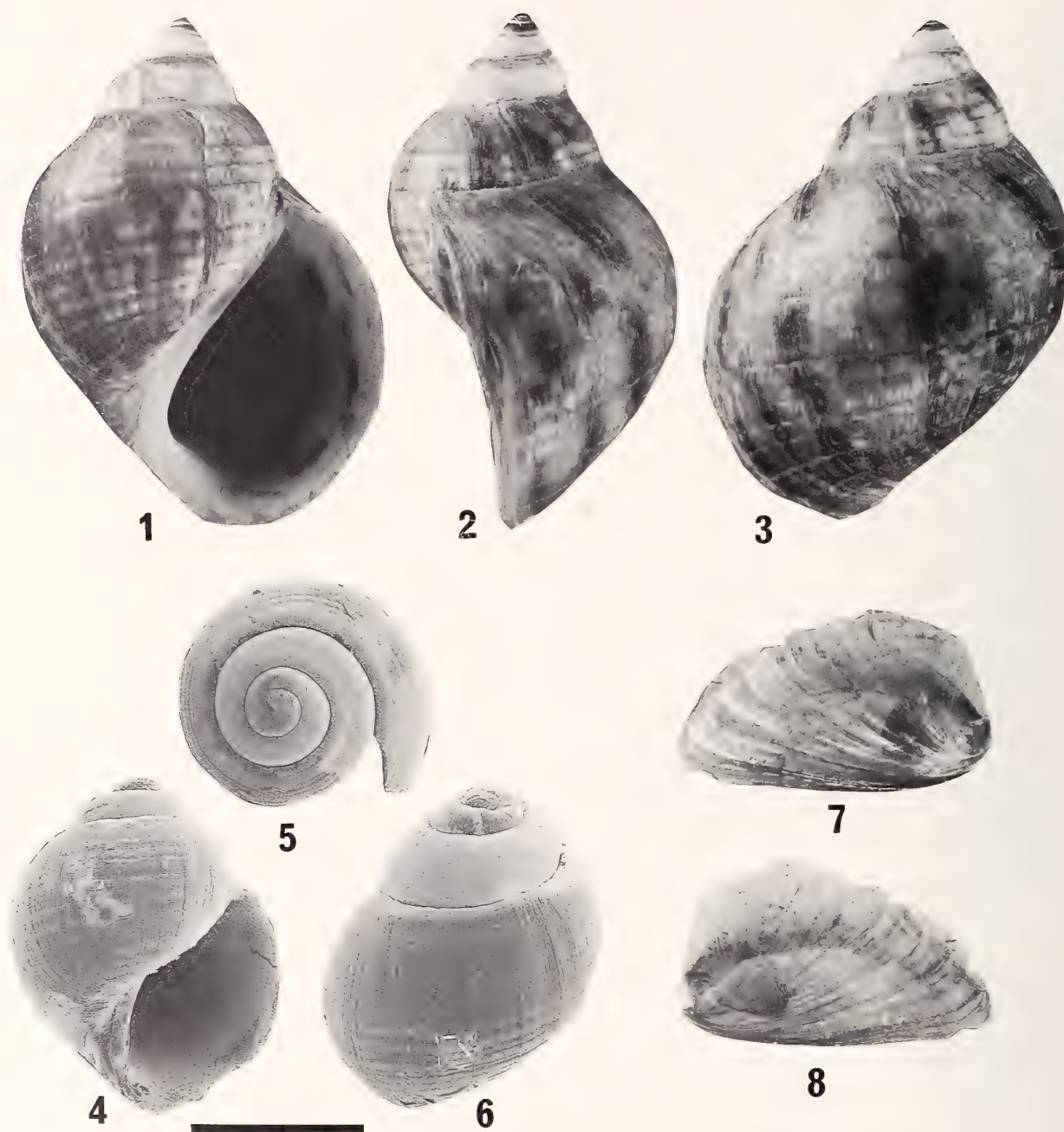
Length	15.8*	14.1	13.8	13.0
Width	9.4*	8.7	9.5	7.7
Aperture length	9.8*	8.6	9.8	8.2
Aperture width	6.2*	5.5	6.2	5.3
Number whorls	5*	5	5	5

shells of developing embryos (Figure 9, emb) can be seen through the swollen, thinly stretched cephalic epithelium covering the head of brooding females.

The mantle cavity is spacious and extends the depth of the first whorl. A ridge-like osphradium flanked with glandular strips on each side is separated from the ctenidium by a wide area of mantle epithelium. The ctenidium (Figure 9, ct) is long and very wide, and has relatively shallow filaments, each comprising a free, fingerlike leading edge and a very broad, shallow attached base. The fingerlike edge is one-half the base length. The rectum (Figure 9, r) is very wide, a little over one-half the ctenidial width, thin-walled, and filled with long, cylindrical fecal pellets stacked in parallel rows and composed of fine sand.

The snout tip has paired fleshy lobes (Figure 9, l) bordering a slitlike mouth. A pair of chitinous jaws lie on the inside of the opening to the oral cavity. The buccal mass is small. The radular ribbon (Figure 10) is broad and short, about 4 mm in length. The rachidian tooth (Figure 12) is triangular shaped, having a flat basal plate with a basal central projection and a pair of basal denticles, each located under and adjacent to the lateral edges of the cutting edge of the tooth, which has a large blunt central cusp flanked on each side by two or three pointed denticles. The lateral tooth (Figures 11–13) is boomerang-shaped, having a basal plate comprising an inner longitudinal pillar and a very long, flat lateral extension, and a cutting edge with a broad, rounded major cusp flanked with an inner pointed denticle and three or four outer pointed denticles. The marginal teeth (Figure 13) have spatulate shafts and broad, sharply folded tips, each with five rounded denticles. The stomach is a large wide organ occupying over one-half the penultimate whorl, and comprising a short style sac and gastric shield.

In females, the subhemocoelic brood pouch consists of invaginated, ciliated, ectodermal epithelium that begins at the brood pore (Figure 9, bp) and extends into the neck and head anteriorly to the tentacular lobes and posteriorly and ventrally throughout the headfoot as far back as the posterior mantle cavity. The brood pouch is completely separate from the cephalic hemocoel, but surrounds the nerve ring and mid-esophagus. Internal folding of the inner epithelium of the brood pouch creates many loculae, each accommodating a developing embryo and communicating



Explanation of Figures 1 to 8

Figures 1-8. *Simulathena papuensis*, sp. nov. Figures 1-3. Holotype AMS C166326, 15.9 × 9.5 mm, Kairuku, Yule Id., Central District, Papua New Guinea. Figures 4-6. Embryonic shells removed from brood pouch showing protoconch, early whorl sculpture, and periostracum (bar = 0.75 mm). Figures 7 and 8. Operculum, 6.7 mm length, showing free (7) and attached (8) sides.

with a common, nearly closed lumen. The brood pouch contains 55-60 embryos, most of which are large and of equal size, but smaller embryos are also randomly distributed throughout the pouch. Before hatching, the em-

bryos have eyes and an operculum and their shells (Figures 4-6) are in an advanced state, attaining 2.25 mm length and having pigment patterns similar to the adult shell and a well-developed periostracum.

Holotype: AMS C166326, length 15.9 mm, width 9.5 mm.

Paratypes: USNM 859456 (two specimens); length 14.7 mm, width 8.7 mm, and length 13.1 mm, width 9.5 mm.

Type locality: Kairuku, Yule Id., Central District, Papua New Guinea (8°50'S, 146°32'E).

Etymology: Named after Papua, where this species was found.

DISCUSSION

The plain, relatively thin shell of *Simulathena papuensis* superficially resembles those of some thiarid and viviparid freshwater snails, but the anatomy differs substantially from that of the viviparids. My initial impression was that this species was an undescribed thiarid; however, close examination of the shell, operculum, and radula indicate that *Simulathena papuensis* has more in common with members of the Planaxidae than with thiarid species. In addition, several anatomical characters point to the Planaxidae as the proper familial assignment.

Shell: The shell sculpture of incised spiral lines and the wide, very shallow anterior canal are common conchological characters of other species of *Planaxis* Lamarck, 1822, *Supplanaxis* Thiele, 1929, and *Holcostoma* Adams & Adams, 1853, and a lenticular rather than ovate operculum (Figures 7, 8) is typical of all planaxids (see HOUBRICK, 1987). The shell shape of *Simulathena*, although unique among planaxids, is most like that of *Holcostoma* species. The periostracum, while relatively thick, is not hispid as in many other planaxid species (see HOUBRICK, 1987).

Anatomy: *Simulathena papuensis* has a number of characters in common with planaxids. The expanded bilobed snout tip is similar to those seen on planaxid species. The radula is closest to those described for species of *Supplanaxis*, *Hinea* Gray, 1847, *Holcostoma*, and *Fossarus* (see HOUBRICK, 1987, 1990). The broad, shallow, ctenidial filaments are similar to those described in *Planaxis sulcatus* (HOUBRICK, 1987:36). The pallial gonoducts are open in contrast to the closed systems found in brooding, parthenogenetic thiarids. It was not determined if *Simulathena* is gonochoristic, but this condition is assumed until proven otherwise. Although the two specimens of *Simulathena* I examined were not preserved well enough to determine the precise pallial oviduct configuration, the large subhemocoelic cephalic brood pouch and the birth pore on the right side of the neck are much like those seen in all other examined planaxid genera (see HOUBRICK, 1987), including *Fossarus*, subfamily Fossariinae (see HOUBRICK, 1990). Similar cephalic brood pouches also occur in many parthenogenetic thiarids (MORRISON, 1954), which are probably a sister group of Planaxidae (see HOUBRICK, 1988).

As mentioned previously, the pair of mantle tentacles projecting from the exhalant siphon is unusual and not

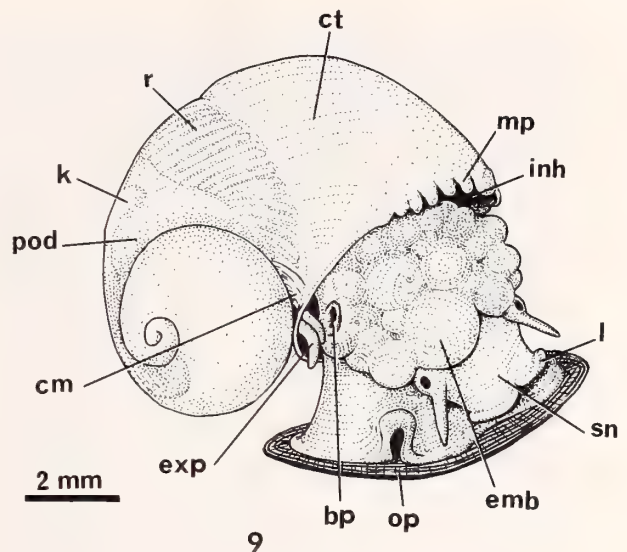
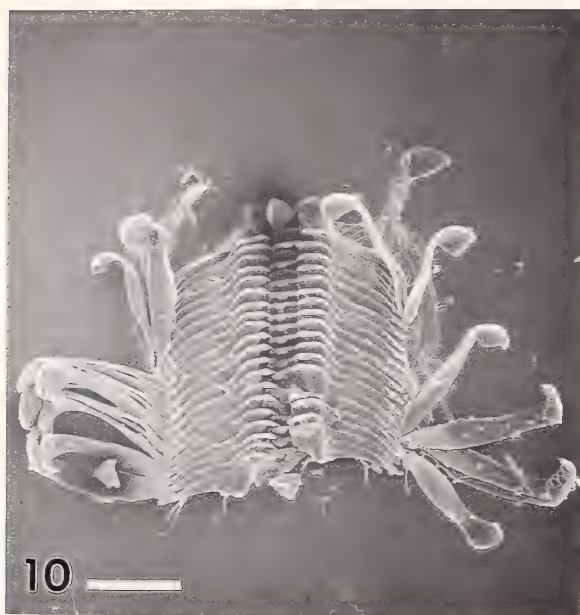


Figure 9

External anatomical features of *Simulathena papuensis*, sp. nov., showing embryos beneath the thin cephalic epithelium of the anterior brood pouch. Legend: bp, brood pore; cm, columellar muscle; ct, ctenidium; emb, embryo inside brood pouch; exp, exhalant papillae; inh, inhalant siphon; k, kidney; l, lobe forming lip of mouth; mp, mantle papillae; op, operculum; pod, pallial oviduct; r, rectum containing fecal pellets; sn, snout.

seen among other planaxids. The wide separation between the osphradium and ctenidium is also a unique feature of *Simulathena*.

Reproductive biology: The most striking external anatomical feature of *Simulathena papuensis* is the enlarged brood pouch extending forward into the head (Figure 9). The brood pouch has a ciliated epithelium and is formed by an ectodermal invagination, as described in other planaxids (see HOUBRICK, 1987). It engulfs much of the cephalic hemocoel, and comprises numerous, thin-walled loculae, all of which communicate with the lumen of the pouch and with each other. Each locula contains or enfolds a single uncapsulated embryo. Embryos presumably enter the brood pouch as fertilized, uncapsulated eggs, and are probably fed on nutritive liquids secreted by the brood pouch walls. They grow to be quite large (up to 2.25 mm in length), presumably emerging through the brood pore as small snails. Most embryos are very large and it is difficult to imagine how they can maneuver through the interstices of the brood pouch and emerge from the small brood pore. It is possible, but unlikely, that they rupture through the thin epithelium of the head and dorsal surface of the neck when they are ready to hatch, although it is unclear what this would do to other, less-developed embryos. Most embryos are roughly the same size, but a number of smaller shelled embryos are present, suggesting that different cohorts are being brooded or that some em-



Explanation of Figures 10 to 13

Figures 10–13. Scanning electron micrographs of various aspects of the radula of *Simulathena papuensis*, sp. nov. Figure 10, bar = 175 μ m; Figure 11, bar = 65 μ m; Figure 12, bar = 25 μ m; Figure 13, bar = 43 μ m.

bryos do not receive the same nourishment from the brood pouch as do others. It is unlikely that the smaller embryos serve as a food source for larger embryos, because they have well-developed shells. The only other planaxid known to brood very large embryos that hatch out as young snails is the Persian Gulf population of *Planaxis sulcatus* (see

THORSON, 1940; BARKATI & AHMED, 1982; HOUBRICK, 1987), in which nurse eggs have been documented.

The large size of the enclosed embryonic snails in *Simulathena papuensis* is unusual among most planaxids, but very large embryos are not uncommon among parthenogenetic thiarids (Houbrick, personal observations).

Ecology: Nothing has been recorded about the microhabitat of this species except that it lives in the intertidal zone.

Geographic distribution: *Simulathena papuensis* is known only from the type locality, but probably occurs in other suitable habitats in New Guinea.

Phylogeny: The original phylogeny of the Planaxidae presented by HOUBRICK (1987:fig. 27) is outdated. *Angiola* Dall, 1926, is now regarded as a synonym of *Hinea*, because *Hinea* has been found to exhibit bioluminescence (PONDER, 1988), which was the only character separating the two genera.

A preliminary updated phylogenetic analysis of the Planaxidae (18 characters, 9 taxa, consistency index = 74) was run, using many of the same characters originally employed by HOUBRICK (1987:48–50) and some modified, revised ones. The revised analysis was done with the Hennig86 algorithm and included new taxa, the Fossarinae, and used *Thiara* Röding, 1798, as the outgroup. The results suggest that *Simulathena* is the sister group of the clade comprising *Hinea*, *Holcostoma*, *Supplanaxis*, and *Fossarus*. This is readily seen by the similarity among the radulae of these taxa. However, final resolution of planaxid phylogeny awaits a more formal cladistic analysis involving many other cerithioidean taxa and a more complete reappraisal of the characters.

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Two New Vitrinellid Species from the Gulf of California, Mexico (Gastropoda: Vitrinellidae)

by

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Abstract. *Cochliolepis cornis*, sp. nov., is described from San Felipe, Baja California, Mexico. This is the first report of the genus in the tropical eastern Pacific. It is compared with *C. parasitica* Stimpson, 1858, type of the genus, and *C. striata* Dall, 1889, both from the tropical western Atlantic. *Cyclostremiscus salvatierrensis*, sp. nov., is also described from the northern Gulf of California; it ranges south to Costa Rica. It is compared with the tropical eastern Pacific species *Cyclostremiscus nummus* and *Cyclostremiscus major*, both of Pilsbry & Olsson, 1952.

INTRODUCTION

MYERS *et al.* (1989) gave a preliminary list of the Vitrinellidae collected by Joyce Gemmell from 1965 to 1976 from San Felipe to San Luis Gonzaga in the northwestern Gulf of California, Mexico. In that report, 25 species were indicated, although five were not identified. Further study of this material has revealed that four of the species were new; two are described in this paper. The other two species have been described by MYERS *et al.* (1991). Other work on the Vitrinellidae from this collection was done by GEMMELL *et al.* (1989) and MYERS *et al.* (1990). Living specimens in this family are seldom collected, and nearly all species descriptions must necessarily be based on shell characters alone.

Institutional abbreviations are as follows: LACM, Los Angeles County Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; SDNHM, San Diego Natural History Museum; USNM, National Museum of Natural History, Smithsonian Institution.

VITRINELLIDAE Bush, 1897

Cochliolepis Stimpson, 1858

Type species: *C. parasitica* Stimpson, 1858, by original designation.

Cochliolepis cornis Hertz, Myers & Gemmell, sp. nov.

(Figures 1-4)

Description: Holotype 4.2 mm diameter, 1.4 mm altitude, thin, white, discoidal, flattened. Almost 2 protoconch whorls,

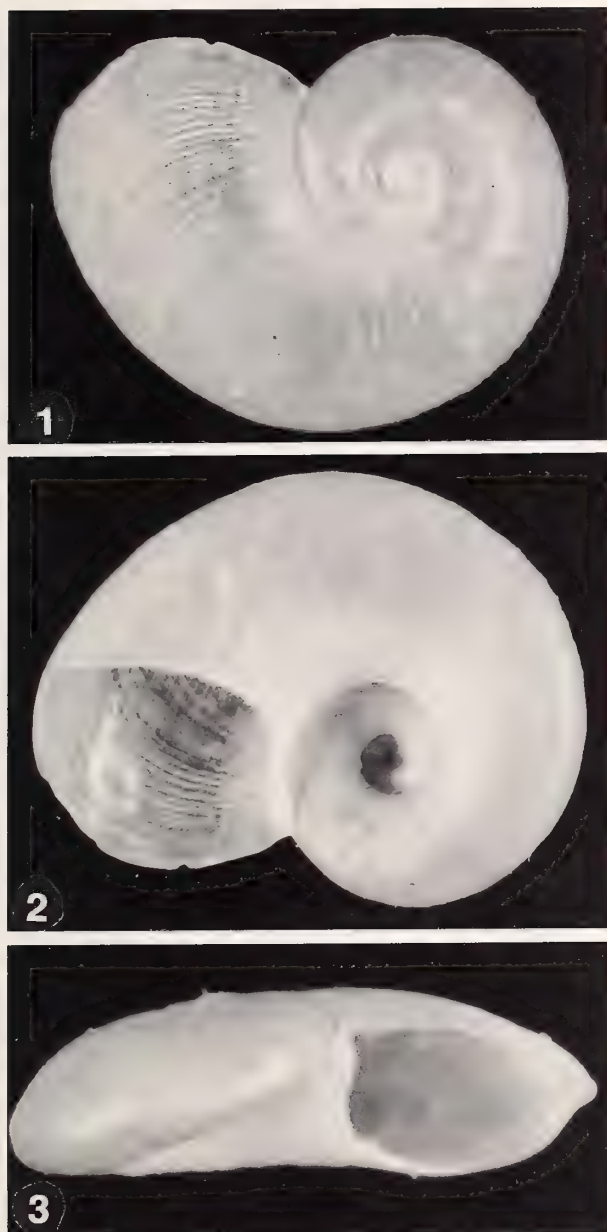
2½ teleoconch whorls. Spire low, projecting, tipped laterally from aperture. Suture well defined, excavated. Whorls rapidly increasing in diameter and coiled like a ram's horn. Umbilicus broadly open, narrowing to apex, revealing rounded surface of whorls. Aperture entire, asymmetric, with very faint sulcus posteriorly, slightly produced at periphery; inner lip reflected, appressed to previous whorl. Under magnification entire surface covered by closely spaced spiral threads with irregularly spaced fine axial growth lines.

Etymology: The name is Latin, "bearing horns," suggested by the ram's-horn coiling of the shell.

Type locality: Bahía San Felipe, Baja California, Mexico (31°03'N, 114°48'W), in drift.

Type material: 36 specimens from type locality, collected by Joyce Gemmell from 1965 to 1976. Holotype: SDNHM 93511. Paratypes: SDNHM 93512, 14 specimens; LACM 2576, 6 specimens; USNM, 8 specimens; SBMNH 35169, 8 specimens. One paratype, dredged by Joyce Gemmell on shrimpboat *Chamizal* on clay bottom in 25 m just south of Puertecitos, Baja California, Mexico (30°18'30"N, 114°37'24"W), 8-10 July 1969, retained in Hertz collection.

Discussion: We have placed this new species in the genus *Cochliolepis* based on the rapidly increasing diameter of the whorls, coiled like a ram's horn, and the umbilicus open to the apex (see GARDNER, 1948; ABBOTT, 1974). GARDNER (1948) redefined the genus *Cochliolepis* and emphasized the "ram's-horn coiling" and wide umbilical fun-



Explanation of Figures 1 to 3

Figures 1–3. *Cochliolepis cornis*, sp. nov. Holotype, SDNHM 93511. Diameter 4.2 mm, altitude 1.4 mm. Bahía San Felipe, Baja California, Mexico, in drift. Figure 1. Dorsal view. Figure 2. Basal view. Figure 3. Apertural view.

nel as diagnostic generic characters. This is the first report of the genus in the eastern Pacific.

Cochliolepis cornis resembles the type species, *C. parasitica*, in having rapidly expanding whorls and similar size, but *C. cornis* differs in having the surface covered by closely spaced spiral threads, whereas *C. parasitica* is smooth except for occasional strong growth lines. *Cochliolepis cor-*

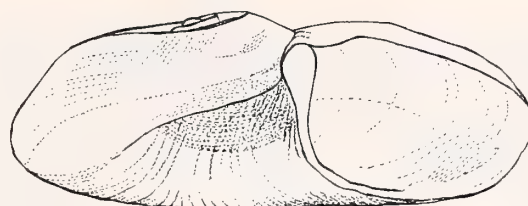


Figure 4

Cochliolepis cornis, sp. nov. Holotype. Camera lucida drawing showing laterally tipped spire and appressed inner lip.

nis has a projecting, tilted protoconch, whereas *C. parasitica* has a depressed protoconch surrounded by a thin, transparent shell layer that extends above the suture of the body whorl, forming what looks like a double suture.

Cochliolepis cornis also resembles *C. striata* Dall, 1889, in shape and its sculpture of closely spaced spiral cords. *Cochliolepis cornis* differs from *C. striata* in its smaller size (*C. striata* attains approximately 6.6 mm diameter) and in having a projecting, tilted protoconch. The protoconch of *C. striata* is partially covered by the succeeding whorl and the body whorl coils slightly above the periphery. In *C. cornis*, the body whorl terminates at the periphery. *Cochliolepis cornis* differs further in having a broadly open umbilicus instead of the constricted umbilicus of *C. striata*.

Cyclostremiscus Pilsbry & Olsson, 1945

Type species: *Vitrinella panamensis* C. B. Adams, 1852, by original designation.

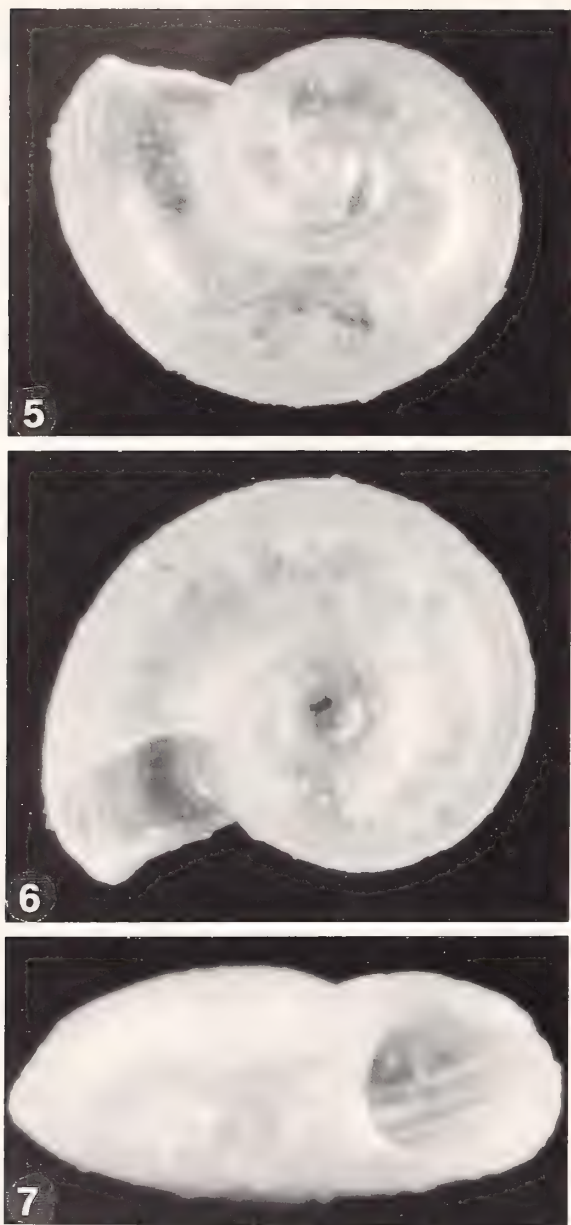
Cyclostremiscus salvatierrensis Hertz,
Myers & Gemmell sp. nov.

(Figures 5–8)

Description: Holotype 1 mm maximum diameter; protoconch of approximately $\frac{1}{2}$ whorl, slightly projecting; $2\frac{1}{4}$ glassy, somewhat flattened teleoconch whorls; suture deeply impressed. Aperture quadrate, with thick parietal callus extending beyond plane of peristome and containing a moderately prominent anal sulcus; lip edge raised and reflected dorsally, slightly produced at termination of first dorsal spiral cord. Body whorl with prominent peripheral cord and three strong, rounded spiral cords above; interspaces narrow; remainder of dorsum smooth. Base having two strong spiral cords, with narrow interspaces below and adjacent to periphery; remainder of base smooth, somewhat rounded, terminating in a moderately open funnel-shaped umbilicus. Axial sculpture lacking except for a few irregularly spaced growth lines.

Etymology: The name derives from Isla Salvatierra, the type locality.

Type locality: One km west of Isla Salvatierra (also known as Isla San Luis), Baja California, Gulf of California,



Explanation of Figures 5 to 7

Figures 5–7. *Cyclostremiscus salvatierrensis*, sp. nov. Holotype, SDNHM 93513. Diameter 1.0 mm, altitude 0.5 mm. West of Isla Salvatierra, Gulf of California, Mexico. Figure 5. Dorsal view. Figure 6. Basal view. Figure 7. Apertural view.

Mexico (29°57'48"N, 114°28'W), in sand with scallop valves in 25 m.

Type material: 2 specimens from type locality, collected by Joyce Gemmell on 8–10 July 1969. Holotype: SDNHM 93513; paratype: USNM, 1 specimen. Nine paratype lots in LACM as follows: LACM 2581 (ex LACM-AHF 237),



Figure 8

Cyclostremiscus salvatierrensis, sp. nov. Holotype. Camera lucida drawing showing the quadrate aperture with thick parietal callus.

1 specimen, Bahía Magdalena, Baja California Sur, Mexico (24°19'15"N, 110°37'30"W); LACM 2585 (ex LACM 66-28), 1 specimen, Bahía Partida, Baja California Sur, Mexico (24°25'N, 110°25'W); LACM 2578 (ex LACM 66-22), 1 specimen, Bahía Muertos, Baja California Sur, Mexico (24°55'N, 109°46'W), in 18–55 m; LACM 2583 (ex LACM 66-21), 3 specimens, off Punta Arena, Baja California Sur, Mexico (23°32'N, 109°28'W) in 18–36 m; LACM 2584 (ex LACM 71-22), 5 specimens, south of Punta Arena (2 km south of Los Tezos Ranch) (23°31'N, 109°W) in 9 m; LACM 2579 (ex LACM 66-19), 1 specimen, Bahía Pulmo, Baja California Sur, Mexico (23°22'N, 109°25'W) in 1–6 m; LACM 2580 (ex LACM 66-20), 1 specimen, south end of Bahía Pulmo, under boat anchorage (23°22'N, 109°25'W) in 6 m; LACM 2577 (ex LACM 68-45), 2 specimens, Bahía Cuastocomate, Jalisco, Mexico (19°13'45"N, 104°44'53"W) in 18–36 m; LACM 2582 (ex LACM-AHF 116-33), 1 broken specimen, south of Puerto Culebra, Costa Rica (10°33'35"N, 85°42'30"W) in 4 m.

Distribution: The new species is known from scattered records from Isla Salvatierra in the northern Gulf of California, Mexico, to Puerto Culebra, Costa Rica.

Discussion: *Cyclostremiscus salvatierrensis* is closest to the eastern Pacific species *C. nummus* and *C. major*, both of Pilsbry & Olsson, 1952. *Cyclostremiscus salvatierrensis* has a somewhat flattened shell with a prominent peripheral cord, whereas *C. nummus* has a tricarinate shape. *Cyclostremiscus salvatierrensis* differs from *C. nummus* in having three cords immediately above the periphery on the body whorl and two immediately below, with the remaining surface smooth, whereas *C. nummus* has spiral cords over the entire surface, three cords being stronger.

Cyclostremiscus salvatierrensis differs from *C. major* in its much smaller size, *C. major* attaining a diameter of 10.9 mm. *Cyclostremiscus salvatierrensis* has six spiral cords whereas *C. major* has spiral cords over the entire shell surface.

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Two Giant African Land Snail Species Spread to Martinique, French West Indies

by

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Abstract. The American tropics, long known to be vulnerable to the depredations of the giant African land snails, have recently been penetrated by *Achatina fulica*, endemic in East Africa, and *Limicolaria aurora*, endemic in West Africa. Both species can produce extraordinarily heavy infestations, cause serious damage to crops, carry agents of human diseases, and aggressively compete with or replace endemic snail species. Concerted efforts are being made to contain the infestations.

For over 40 years, the giant African land snail, *Achatina fulica* Bowdich, 1822 (normally 9–15 cm in length) has been documented as the world's largest, most economically important snail pest in agriculture and horticulture (MEAD, 1961). Further, it is known to be a vector of two disease agents in humans: the rat lungworm *Angiostrongylus cantonensis*, causing eosinophilic meningoencephalitis (WALLACE & ROSEN, 1969; ASSI ADOU *et al.* 1980; PERERA *et al.*, 1983; PEREZ MARTIN *et al.*, 1984; ANDERSEN *et al.*, 1986), and a gram-negative bacterium, *Aeromonas hydrophila*, causing a remarkably wide range of symptoms, particularly in persons on immunosuppressant drugs (DEAN *et al.*, 1970).

In prehistoric times, specimens of this species were carried from their native home in East Africa to Madagascar, either accidentally or for food. Nearly 200 yr ago, they were introduced from there to the small island groups in the Indian Ocean for medicinal and other purposes. And from there naturalists introduced them to India and Ceylon. By the 1930s they had spread rapidly through tropical and subtropical East Asia. World War II and the postwar activities spread the infestations to many Pacific islands and interceptions were made in Australian, Canadian, and U.S. ports, including those in Hawaii. It is enigmatic that during all this time, *Achatina fulica* is still not believed to

have become established anywhere in Central or South America, with their wide array of apparently ideal environments. Now, however, we are seeing the first penetration of the American tropics by this and one other species of the family Achatinidae.

In 1984, *Achatina fulica* (Figure 1) was found established in Guadeloupe, French West Indies, in Cascade aux Ecrevisses, a scenic area in the rain forest of Basse Terre, the volcanic part of the island (FRANKIEL, 1989). Other than the fact that the site is a tourist attraction, there is no indication how, why, or exactly when the species got there. It is most probable that someone who came into possession of one or more specimens in travel, through the mails, or in delivered produce decided the site was suitable for abandonment. The first extension of this infestation was found in 1987 in Sainte Anne on Grande Terre, the calcareous part of the island. Soon after, the snails spread to a number of sites in both parts of the island. A documentary television film was prepared by the local authorities to alert the people to the problem.

In August 1988, this film was aired in Martinique, about 200 km south of Guadeloupe. Responding to this, a teacher in Morne Rouge, a village at the foot of Mt. Pelée at the north end of the island, notified the authorities that *Achatina fulica* was in a local banana plantation. In-



Figure 1

Nearly full-grown specimen of *Achatina fulica* from Morne Rouge, Martinique, FWI, about 12 cm shell length, 7 whorls, black body.

spection confirmed the infestation (SCHOTMAN, 1990), but no discernible damage was observed in the plantations or in the cultivated pastures. According to the local people, the first specimens were believed to have been brought to Martinique in July 1988, by a family from an infested area in Les Abymes, Guadeloupe. A television documentary film showing this new infestation on Martinique was prepared at the request of the junior author, who urged the people in January 1989 to report any other possible infestation site. Such a site was reported by the directress of a day nursery in Saint Esprit, a village in the south part of the island. The snails, however, appeared different.

Specimens were sent to Simon Tillier of the Museum National d'Histoire Naturelle (Paris) and were forwarded to the senior author. On the basis of the soft anatomy, these proved to be *Limicolaria aurora* (Jay, 1839), a common, small (4.5–6 cm in length), spotted or completely pale West African species found from Guinea to Gabon (Figure 2). The infestation appears to be limited to about 500 m along the river Saint Esprit, involving about 12 hectares. In contrast to the experience with *Achatina fulica* in Morne Rouge, at the start of the rainy season in August 1989, *L. aurora* appeared in considerable numbers, attacking yam, bean, pepper, Jerusalem artichoke, cucum-

ber, okra, and sweet potato. Inquiries suggest these snails were introduced some time after 1986 by Martinicans who lived in Africa and probably consumed them. This infestation is the first record for *Limicolaria* outside Africa and its coastal islands. In Cameroon, this species causes damage to palm fruits and leguminous cover crops (SPENCE, 1938).

Just as soon as this snail was properly identified, the Secretariat of the Caribbean Plant Protection Commission (CPPC) was notified. This agency in turn notified all member countries. In addition, at the ninth session of the CPPC in October 1989, in Trinidad and Tobago, the junior author reminded the conferees that *Achatina fulica* is in Guadeloupe and that both *A. fulica* and *Limicolaria aurora* are in Martinique. Assistance was formally requested by the Federation Departementale des Groupements de Defense Contre les Ennemis des Cultures de la Martinique. Because Morne Rouge is a valuable center for commercial cut-flowers destined for U.S. markets, there is great concern that the trade may be in jeopardy of U.S. plant quarantines. Hence, the Service de la Protection des Végétaux has vigorously pursued a plan of attack for the eradication of the small population of *A. fulica* of Morne Rouge. The program calls for (1) exhaustive search-and-destruction in the infested area, (2) intensive surveillance in the contam-



Figure 2

Full-grown specimen of *Limicolaria aurora* from Saint Esprit, Martinique, FWI, about 6 cm shell length, 9 whorls, striped yellow-tan body.

inated, intermediate security, and uncontaminated zones, and (3) molluscicidal attack through the use of metaldehyde, thiodicarb, and mercaptodimethur. The same strategy has been established for *L. aurora* in Saint Esprit. Biological control through the use of the predatory snails *Euglandina rosea* (Ferussac) and *Gonaxis quadrilateralis* (Preston) has not received serious consideration because of the sad experiences of having these and other predators destroy to extinction zoogeographically important endemic snails in Hawaii, Tahiti, New Caledonia, and other Pacific island groups (VAN DER SCHALIE, 1969; HART, 1978; HADFIELD & KAY, 1981; CLARKE *et al.*, 1984; POINTIER & BLANC, 1985). Although both *A. fulica* and *L. aurora* are choice items for human consumption in Africa (PILSBRY, 1919; CANSDALE, 1940) and are safe to eat if they are adequately cooked, the authorities have not attempted biological control through encouraging the local people to consume them because it is widely known among the people that snails are carriers of diseases. Further, counter to the control program, collecting the snails and taking them home to be eaten could enhance dissemination in the island and invite their spread to other islands.

The successful establishment of these two pestiferous snails in the Caribbean belatedly demonstrates the predicted vulnerability of this area (MEAD, 1973). It is certain

that unless these infestations are contained, further accidental and incidental spreading, like that from Guadeloupe to Martinique, will continue to take place, eventually extending to tropical and subtropical Central and South America. Records show the snails have a long list of acceptable food plants. New ones will be added. It is not yet known whether the snails in these new infestations are carrying the rat lungworm *Angiostrongylus cantonensis*; but this parasite has been reported from West Africa, the Indo-Pacific, and recently Cuba and Puerto Rico (WALLACE & ROSEN, 1969; ASSI ADOU *et al.* 1980; PEREZ MARTIN *et al.*, 1984; ANDERSEN *et al.*, 1986). Therefore, from the public-health standpoint, it should be assumed to be present in the Martinique and Guadeloupe snail populations. That these two snail pests could serve as novel intermediate hosts for some endemic and introduced parasites is likely. Beyond attacking plants and carrying diseases, the sheer numbers of individuals in their mature populations provide a serious nuisance to the human population. As vigorous, aggressive species, they will provide competition to and even replacement of endemic species. Paradoxically, the smaller *Limicolaria aurora* may prove eventually to be the worse pest.

With the probable exceptions of California and Florida, no region in the world has had greater, more diversified

experience with plant quarantines and control measures then the state of Hawaii. With considerable federal, state, and private funds, and with concerted efforts of professional personnel, that state was able to confine *Achatina fulica* to the two original infested islands of Oahu and Maui between the years 1936 and 1950. After that, the giant snail made the predicted, relentless progress to all of the other main islands in the archipelago. However, the history of the infestation and final eradication of this snail in southern Florida and in northeastern Australia are in contrast for a number of important reasons (COLMAN, 1977, 1978; MEAD, 1979). With these earlier examples as guides, the authorities throughout the Caribbean must promulgate carefully considered external and internal quarantines and control measures to contain the spread of these two plant pests. Eradication has been proven possible, but adequate funds are absolutely vital. Regrettably, the inexorable time factor continues to intensify the urgency to take effective measures while the infestations are still somewhat limited.

Voucher specimens of *Achatina fulica* and *Limicolaria aurora*, respectively are deposited in the Muséum National d'Histoire Naturelle, Paris (unnumbered); National Museum of Natural History, Washington, D.C. (USNM 860572, 860571); and Museum of Natural History, Santa Barbara, California (SBMNH 35522, 35523).

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Reproductive Biology of *Vermetus* sp. and *Dendropoma corrodens* (Orbigny, 1842): Two Vermetid Gastropods from the Southern Caribbean

by

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Abstract. A comparison of the reproduction of two Venezuelan vermetids is presented. *Vermetus* sp. lives attached to hard substrates, up to 5 m in depth and occurs in decreasing densities with increasing depth, from 30 individuals/m² at sea level to 9 individuals/m² at 5 m. *Dendropoma corrodens* encrusts calcareous rocks in very shallow waters at densities of 130,000 individuals/m² (mean values). Both species reproduce throughout the year. *Vermetus* sp. broods up to 54 egg capsules in the mantle cavity, each containing 289 ± 114 eggs that measure 240 ± 14 μ m in diameter. Only 188 ± 87 embryos developed to veliger larvae, with shells measuring 454 ± 20 μ m in diameter at hatching; the remaining eggs are nurse eggs. *Dendropoma corrodens* broods up to 8 egg capsules in the mantle cavity, each containing 8 ± 1.1 eggs measuring 276 ± 25 μ m. A single egg in each capsule disintegrates, and its yolk is ingested by the developing embryos, which hatch as crawling juveniles with shells measuring 512 ± 59 μ m. A summary of reproductive aspects of the family Vermetidae is given.

INTRODUCTION

Vermetids are abundant in the intertidal zone of warm-temperate to tropical seas (KEEN, 1961). They constitute a morphologically distinct group among gastropods, characterized by an uncoiled shell attached to or buried in the substrate and having mobility only in the early, hatched stages. The larva or juvenile settles to a suitable substrate and attaches; its adult shell then grows in a coil around an axis at a 90° angle to that of the larval shell (KEEN, 1961).

As a consequence of sessile life, vermetids show some modifications in feeding and reproduction. The vermetid reproductive system has been described in detail by MORTON (1951, 1965) and HADFIELD (1970). HADFIELD (1969) presented information related to spermatophore structure, and HADFIELD & HOPPER (1980) extensively described the male reproductive systems and spermatophoral organs from seven Hawaiian and Californian species in three genera. SCHEUWIMMER (1979, 1981) studied sperm dimorphism and sperm transfer in the vermetid *Serpulorbis imbricatus*.

In the four vermetid genera that have been studied, *Dendropoma*, *Petalconchus*, *Serpulorbis*, and *Vermetus*, there

are two ways in which egg capsules are brooded: (1) free inside the mantle cavity, as reported by HADFIELD *et al.* (1972) for *D. gregaria*, *D. platypus*, *D. ryssaconcha*, *D. psaroccephala*, *P. montereyensis*, and *V. alii*, by HUGHES (1978a) for *D. corallinaceum*, and by MORTON (1965) for *D. irregulare*, *D. marchadi*, and *D. tholia*; or (2) attached to the internal side of the shell and suspended in the mantle cavity as reported by HADFIELD *et al.* (1972) for *S. variabilis*, *D. meroclista*, and *P. keenae*, by HUGHES (1978b) for *S. aureus*, by HUGHES (1978a) for *S. natalensis*, by HUGHES & LEWIS (1974) for *D. maximum*, by BANDEL (1976) for *P. erectus* and *P. mcgintyi*, by MORTON (1951) for *S. zelandicus*, and by MORTON (1965) for *V. triquetra*.

BARASH and ZENZIPER (1985) presented a review of the structural diversity and adaptative characters of the Vermetidae. In Hawaii, HOPPER (1981) studied the ecology and reproductive biology of some vermetid gastropods by comparing the dynamics and reproduction of populations that occupy the same or different habitats and the relation between life-history characteristics and female body size. In the Colombian southern Caribbean, BANDEL (1975a) studied some aspects of the reproduction of two species of *Petalconchus* (*P. erectus* and *P. mcgintyi*). HADFIELD (1989) and HADFIELD & IAEA (1989) presented detailed infor-

mation on the reproduction of *Petalconchus montereyensis* from two populations (Washington and California) and discussed the effects that these two different latitudes may have on juvenile size and fecundity in the species. SAFRIEL & HADFIELD (1988) also studied in detail some ecological and reproductive aspects of *Dendropoma meroclista* and an apparent sibling species. In this paper we will describe two Venezuelan vermetids, *Vermetus* sp. and *Dendropoma corrodens*, and discuss their reproductive biology concerning brooding, type of development, and embryonic nutrition.

MATERIALS AND METHODS

A population of *Vermetus* sp. was located in Puerto Cabello, Venezuela, living attached to the walls of the Planta Centro power plant cooling-water intake channel (10°30'6"N, 68°9'36"W). This vermetid is found at the intertidal zone and at all depths in the channel (0–5 m). A *Dendropoma corrodens* population was located in Morrocoy National Park at Punta Mayorquina (10°53'45"N, 68°13'48"W), encrusting dead coral in shallow waters of the intertidal zone, at a maximum depth of 0.70 m (Figure 1).

From January to December 1986, monthly collections of both species were made at each site. Ten adult (total = 110) specimens of *Vermetus* sp. were collected and transported to the laboratory in individual plastic bags with seawater, and two to three rocks colonized by *Dendropoma corrodens* were collected and taken to the laboratory in an ice-chest with seawater. Once in the laboratory, the two species were maintained separately; each individual of *Vermetus* sp. was kept in a 300-mL beaker.

The following aspects were studied for both species:

- (1) Localization of egg capsules within the female and brooding type.
- (2) Number and size of egg capsules per female.
- (3) Identification of the stages of the embryos inside the egg capsules.
- (4) Number of eggs and embryos per egg capsule and their size.
- (5) Time of embryonic development from egg to hatching, by reconstructing experimentally developing series starting from known stages of development. The egg capsules were separated according to the stage of their embryos and kept in 100-mL beakers inside an aquarium with Millipore-filtered (Whatman GF B) seawater. The egg capsules were incubated at 27°C in a Precision (818) Incubator; air was supplied by an air-pump and capsules were kept in complete darkness. Observations of the embryos inside the egg capsules and the substitution of filtered seawater were done daily. At hatching, the type of development was noted (direct to crawling juvenile or indirect to veliger larva).
- (6) Histological study of the gonads by standard paraffin techniques and hematoxylin-eosin staining.

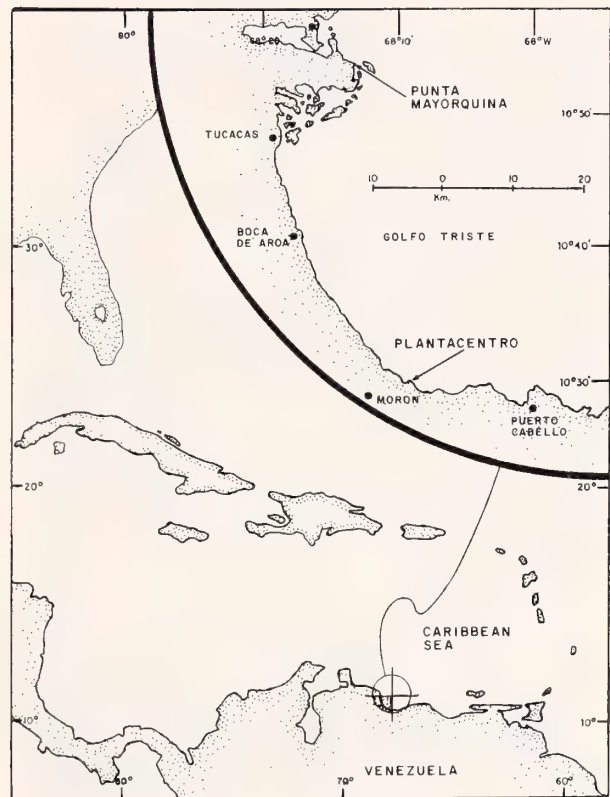


Figure 1

Map of the Caribbean showing study areas: Planta Centro power plant and Punta Mayorquina.

Physical parameters recorded monthly at each locality were temperature, salinity, and suspended solids in water (using the standard gravimetric technique described in APHA *et al.*, 1985).

RESULTS

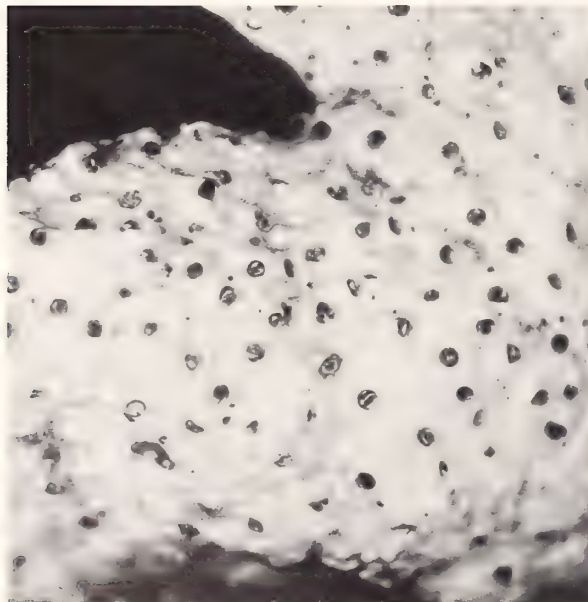
Habitat

Vermetus sp.: This vermetid was found at all depths on the power plant channel wall at population densities ranging from 29.9 ± 7.1 individuals/m² in the shallow areas (to 1 m depth) to 9.1 ± 4.6 individuals/m² in the deeper areas (to 5 m depth). Temperatures varied from 26.4°C (January) to 30°C (April), salinity varied between 34 and 36 ppt, and organic suspended matter varied from 1.7 (February) to 21.8 (April) mg/L. The annual mean value of organic suspended matter was 6.21 ± 6.04 mg/L. This high variance is due to an enormous input of organic matter brought by an adjacent stream (Quebrada El Palito) after a strong rain over its headwaters in April, which marks the beginning of the rainy season (April to September).

Dendropoma corrodens: This species is entrenched in coral rocks at a population density of 12.6 ± 4.8 individuals/cm² at the collection site. Temperatures varied from



a. 1 cm



b. 1 cm

27 to 35°C within a single day, but were generally warmest during May–September and coldest during October–February. Salinity varied between 34 and 36 ppt, and organic suspended matter varied from 0.2 mg/L (February) to 7.5 mg/L (April). The annual mean value of organic suspended matter was 1.79 ± 2.07 mg/L, and as in the *Vermetus* area, a considerable input of organic matter was caused by flooding of the stream.

Species Description

Vermetus sp.: Material has been deposited in the American Museum of Natural History, New York (catalogue number 232098).

The attached adult shell is 2.5 to 7.0 cm (mean = 4.8 ± 1.0 cm, $n = 107$) in length and 2.0 to 4.4 cm (mean = 2.9 ± 0.5 cm, $n = 75$) in width. The unattached tube grows perpendicular to the substrate and ranges from 1 to 12 cm in length (mean = 3.6 ± 1.9 cm, $n = 106$) with a maximum opening of 1.2 cm in diameter. The coil ranges from 5 to 9 whorls ($n = 75$). The shell's exterior is dark gray with thicker lines that are perpendicular to the direction of growth; the inside of the shell is smooth and light brown (Figure 2a). The soft bodies are dark red-wine in color, and the cephalic region is distinguished by the presence of small white spots. The adult body length ranges from 5.0 to 14.1 cm (mean = 8.4 ± 1.8 cm, $n = 102$), and the diameter of the anterior region ranges from 0.4 to 1.1 cm (mean = 0.7 ± 0.1 cm, $n = 102$). The operculum is concave and brown, and measures 0.3 to 0.6 cm in diameter (mean = 0.5 ± 0.1 cm, $n = 102$). The rachidian tooth of the radula has a trapezoidal shape with two prominent peaks at the base.

Dendropoma corrodens: The shell is entrenched in the coral substrate, which is generally covered by calcareous algae (*Lithothamnium*) (Figure 2b). The shell aperture measures 1.5 ± 0.1 mm ($n = 102$). The inside of the shell is smooth and dark red-wine in color near the aperture and cream-beige in the interior. The diameter of the coil ranges between 3.6 and 3.7 mm. The adult body length ranges from 3.8 to 13.5 mm (mean = 9.2 ± 1.8 mm, $n = 121$); the diameter of the anterior region ranges from 0.7 to 1.8 mm (mean = 1.3 ± 0.2 mm, $n = 118$); the anterior region is brown with white and yellow spots on the cephalic region. The operculum is convex and dome shaped, with concentric rings; it is reddish brown and ranges in diameter from 0.7 to 1.8 mm (mean = 1.3 ± 0.2 mm, $n = 102$). The rachidian tooth of the radula has a rectangular shape.

Figure 2

Figure 2a. Adult specimen of *Vermetus* sp.

Figure 2b. Specimens of *Dendropoma corrodens* settled on *Lithothamnium* substrate.

Table 1

Vermetus sp. Characteristics of embryonic development: stages I, II, III, and IV.

Stage	Capsules diameter (mm) mean \pm SD (n)	Number of developing embryos per capsule mean \pm SD (n)	Size of embryos (μ m) mean \pm SD (n)	Number of days to reach each stage (from stage I)	Characteristics of embryos
I	2.32 \pm 0.38 (97)	289 \pm 114 (33)	240 \pm 14 (401)	0 (initial stage)	Yellow round eggs.
II	2.64 \pm 0.49 (79)	254 \pm 72 (28)	340 \pm 30 (320)	4	Trochophore larvae. Signs of moving. Small cilia. Ocular spots.
III	2.93 \pm 0.42 (96)	181 \pm 83 (25)	395 \pm 21 (255)	9	Early veliger larvae. Light yellow fragile shell. Packed yolk inside larvae. Small velum. Eyes. Cephalic tentacles.
IV	3.42 \pm 0.45 (51)	188 \pm 87 (4)	454 \pm 20 (55)	14	Late veliger larvae. Well developed brown shell. Big velum. Internal yolk almost totally consumed.

Reproduction

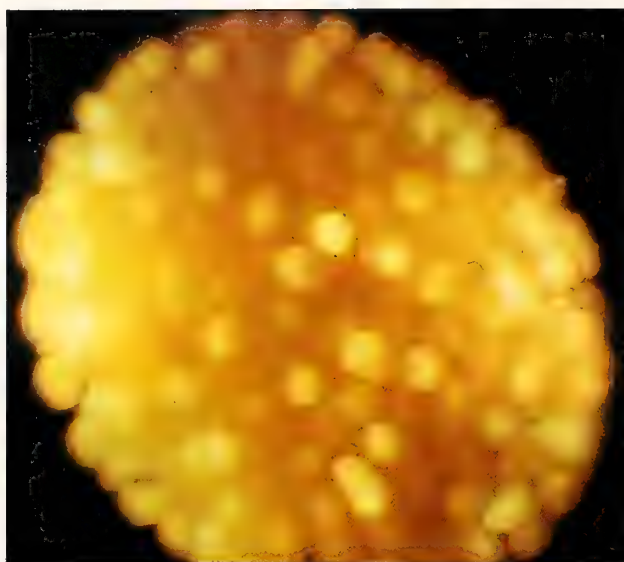
Both species are gonochoristic and reproduce throughout the year. The collected females had brooded egg capsules containing eggs and embryos in every month. Histological analysis of the gonads showed all stages of sexual maturity in both females and males in each collection throughout the year.

Vermetus sp.: The female broods up to 54 spherical egg capsules in the mantle cavity (mean = 19.1 \pm 13.1, n = 49). No relationship was found between female size and the number of egg capsules brooded (Kendall correlation coefficient, P > 0.05, n = 49). The embryos inside the egg capsules were at different stages of development; these stages were classified in order of development from egg to hatching as I, II, III, and IV, or egg, trochophore larva, early veliger larva, and late veliger larva respectively (Table 1). Each capsule contains embryos at the same stage of development, but one female may be brooding embryos at different stages at the same time.

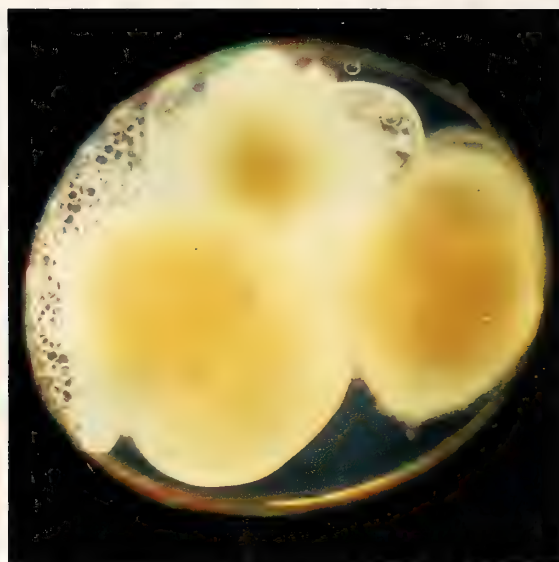
In stage I, the egg capsules measure 2.3 \pm 0.4 mm in diameter and contain 289 \pm 114 eggs. The eggs are round and yellow, and measure 240 \pm 14 μ m in length. The time to reach the next stage is four days, but after the first day the embryos are no longer round. In stage II, the egg capsules measure 2.6 \pm 0.5 mm in diameter and contain 254 \pm 72 trochophore larvae measuring 340 \pm 30 μ m in length. These larvae show signs of movement due to the presence of small cilia in the site where the two lobes of the velum will later develop. Ocular spots are distinguish-

able at this stage (Figure 3a). The duration of embryonic development in stage II is five days. In stage III, the egg capsules measure 2.9 \pm 0.4 mm in diameter. These capsules contain 181 \pm 83 early veliger larvae with light yellow, fragile shells measuring 395 \pm 21 μ m in length. The velum measures 183 \times 94 μ m in anteroposterior diameter. A large amount of packed yolk can be observed on the inside of the larva. The eyes are distinguishable at this stage (Figure 4a). The duration of stage III is five days. In stage IV, the egg capsules measure 3.4 \pm 0.5 mm in diameter and contain 188 \pm 87 late veliger larvae measuring 454 \pm 20 μ m in length; these larvae have a well developed brown shell with two coils, and the velum measures 279 \times 127 μ m (Figure 3c). At this stage the larval yolk is almost totally consumed (Figure 4b). The veliger larva will remain inside the egg capsule for five days until it hatches.

The difference between the number of eggs in stage I and the number of hatching larvae is due to the presence of nurse eggs, which stop their development in an early stage. Early veliger larvae (stage III) and late veliger larvae (stage IV) were observed eating nurse eggs. (The breaking of the nurse eggs is apparently done by the action of oral cilia and it seems that the beating of the velum cilia also helps in the disintegration of the yolk.) The percentage of eggs that develop to veliger larvae ranges from 62 to 66% (100–107 nurse eggs/capsule). Not all the nurse eggs are consumed at hatching and 4 to 30 eggs remain within the capsule. Figure 3c shows the compact mass of nurse eggs



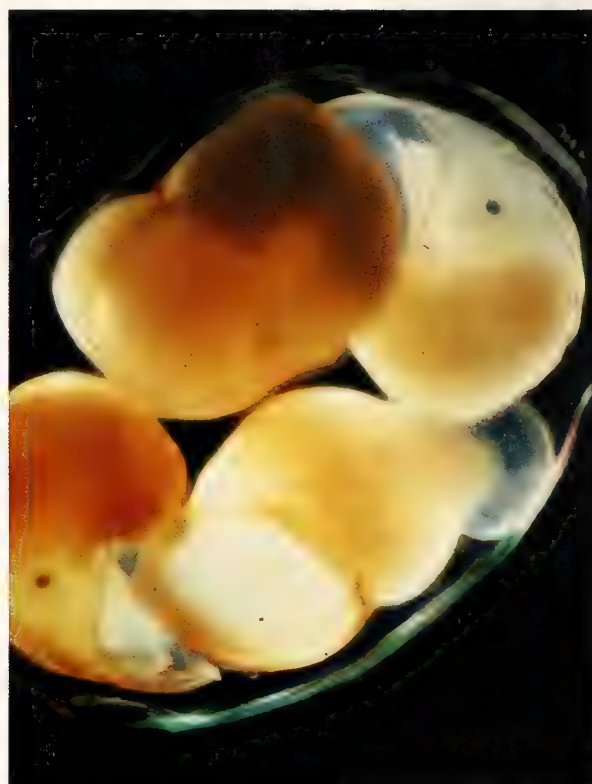
a. 0.5 mm



b. 0.1 mm



c. 0.5 mm



d. 0.1 mm

Figure 3

Figure 3a. Egg capsule of *Vermetus* sp. Embryos in stage II.

Figure 3b. Egg capsule of *Dendropoma corrodens*. Embryos in stage II.

Figure 3c. Egg capsule of *Vermetus* sp. Embryos in stage IV. Detail of the compact mass of nurse eggs and veliger larvae.

Figure 3d. Egg capsule of *Dendropoma corrodens*. Embryos between stages III and IV.

that remain at stage IV. The veliger larva that hatches is positively phototropic and settles within 24 hr; once settled, it resorbs the velum and secretes a calcareous tube (Figure 4c). At this stage the pedal and cephalic tentacles are visible. The shell of a newly settled juvenile measures about 465 μm . The period between stage I and settlement is 20 days.

In some of the veliger larvae, signs of abnormality were observed as an absence of shell coiling. The rest of the structures were normal, including the size of the velum and its movement. The significance of this shell variation is not clear, and settlement of these larvae under laboratory conditions did not occur.

Dendropoma corrodens: The female broods up to eight oval-shaped egg capsules at once in the mantle cavity (mean = 3.6 ± 2.0 , $n = 27$). No relationship was found between the number of capsules and the size of the female (Kendall correlation coefficient, $P > 0.05$, $n = 27$). As in *Vermetus* sp., capsules are found containing embryos at different stages of development in the same female. These stages were also classified as I, II, III, and IV, or egg, trochophore larva, early veliger larva, and crawling juvenile, respectively (Table 2).

In stage I, egg capsules measure $771 \pm 113 \mu\text{m}$ in length and contain 8.0 ± 1.1 eggs; these eggs are round and cream-beige in color and measure $276 \pm 25 \mu\text{m}$ in diameter. In stage II, egg capsules measure $850 \pm 127 \mu\text{m}$ and contain 6.7 ± 1.4 trochophore larvae measuring $329 \pm 46 \mu\text{m}$ in length (Figure 3b). In stage III, egg capsules measure $1120 \pm 58 \mu\text{m}$ and contain 6.3 ± 1.9 larvae with shells measuring $465 \pm 54 \mu\text{m}$ in length; these larvae have a velum, a foot covered by the operculum, and cephalic tentacles (Figure 5a). In stage IV, egg capsules measure $1099 \pm 132 \mu\text{m}$ and contain 6.3 ± 1.8 juveniles measuring $512 \pm 59 \mu\text{m}$; these juveniles have resorbed the velum (Figure 3d). Once the juveniles hatch (Figure 5b), they crawl from their brooding site to the adjacent substrate (Figure 4c). *Dendropoma corrodens* crawling juveniles present two color morphs: 92.5% are white and 7.5% are brown. The time of development from egg to hatching could not be determined as in *Vermetus* sp. because the embryos inside the egg capsules die within hours outside the female's mantle cavity.

The existence of nurse eggs was determined for *Dendropoma corrodens*. The first piece of evidence is a significant difference (Kruskal-Wallis and Tukey multiple comparisons, $P < 0.05$) between the number of embryos per capsule in the first stage as compared to the other three stages. The number of capsules with embryos in stages I, II, III, and IV that were counted for the Kruskal-Wallis test is given in Table 2. The second piece of evidence is that, after stage I and within a few hours of development from egg to trochophore larvae, a small amount of disintegrated yolk can be observed (Figure 3b). This yolk has been totally consumed at stage III. The percentage of individuals that reach the final stage and hatch is 78 to 79%.

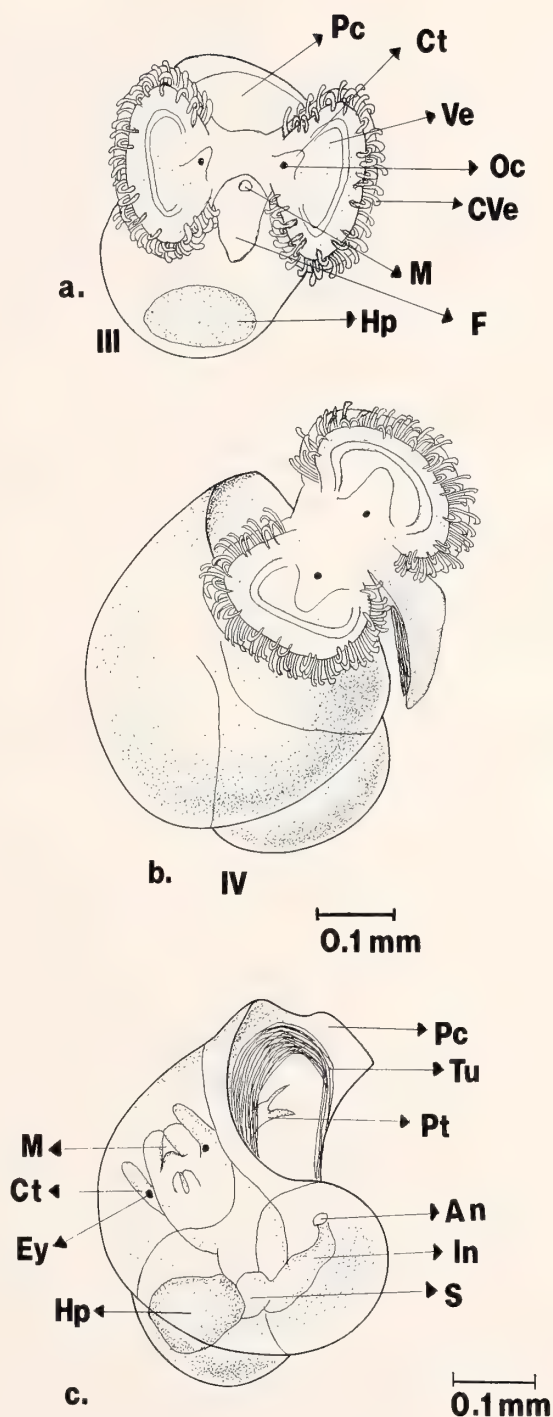


Figure 4

Vermetus sp. a. Early veliger larva, stage III. b. Late veliger larva, stage IV. c. Juvenile, having fixed to the substrate. Key: An, anus; Cm, columella; Cs, cilia of stomach; Ct, cephalic tentacles; CVe, cilia of velum; Eso, esophagus; Ey, eye; F, foot; H, heart; Hp, hepatopancreas (digestive gland); In, intestine; M, mouth; Oc, ocellus; Op, operculum; Pc, protoconch; Pt, pedal tentacles; S, stomach; Tu, tube; Ve, velum.

Table 2

Dendropoma corrodens. Characteristics of embryonic development: stages I, II, III, and IV.

Stage	Capsules diameter (μm) mean \pm SD (n)		Number of developing em- bryos per capsule mean \pm SD (n)	Size of embryos (μm) mean \pm SD (n)	Characteristics of embryos
	Length	Width			
I	771 \pm 113 (13)	695 \pm 94 (13)	8.0 \pm 1.1 (12)	276 \pm 25 (30)	Light yellow round eggs.
II	850 \pm 127 (26)	683 \pm 97 (26)	6.7 \pm 1.4 (25)	329 \pm 46 (66)	Trochophore larvae. Signs of moving. Small cilia. Ocular spots.
III	1120 \pm 58 (23)	812 \pm 82 (23)	6.3 \pm 1.9 (27)	465 \pm 54 (135)	Early veliger larvae. White-yellow fragile shell. Packed yolk inside larvae. Small velum. Eyes. Foot covered by operculum. Cephalic tentacles.
IV	1099 \pm 132 (19)	835 \pm 100 (19)	6.3 \pm 1.8 (28)	512 \pm 59 (134)	Crawling juvenile. Well developed brown or white-yellow shell. No velum. Well developed foot.

DISCUSSION

Vermetus sp. exploits a very special habitat, a fouling community that has developed on two walls (450 m each and 5 to 6 m depth) of a power plant water intake. The most abundant species in the power plant channel are colonial tunicates, bryozoans, cirripedes, sea anemones, polychaetes (sabellids, serpulids, and spirorbids), hydrozoans, sponges, and algae. In field experiments done to determine the frequency of recruitment of different species established in the power plant channel on Plexiglas® plates of 10 \times 10 cm², LOSADA *et al.* (1986) found that, for the period July 1985 to March 1986, vermetid larvae settled on 56% of the Plexiglas® plates placed near our collection site at an intensity classified as "frequent" (between 12.6 and 62.5% of total species settled on the plate). However, they could not distinguish between the larvae of *Vermetus* sp. and *Petalochonchus varians*, which is another vermetid that lives on the channel wall.

The high fecundity of *Vermetus* probably compensates for the great mortality of the hatching veliger larvae, which settle within a period of 24 hr. No significant difference was found between the shell size of the hatching veliger and the settled juvenile; this indicates, as suggested by SAFRIEL & HADFIELD (1988) for *Dendropoma meroclista*, that the larva reside too briefly in the plankton for planktotrophy to be effective. With normal functioning of the power plant, the measured current speed was 0.20 m/sec, so it takes about 37 min to go from the sea entrance to the

inside of the power plant's machinery, where high temperature, mechanical stress, and chlorine application cause high mortality in larval populations. Under these conditions, the local population of *Vermetus* sp. can be maintained by two ways. The first is that vermetid larvae settling on the channel walls may be brought by sea from another, relatively close population of *Vermetus* sp. This is very possible because we noted high densities of this species on the deck of the petroleum refinery El Palito, located about 1 km east and upcurrent of the power plant. The second way is that larvae produced by the vermetid population are able to settle before entering the power plant machinery. LOSADA *et al.* (1986) mentioned that the spatial heterogeneity generated by the development of a fouling community on the channel walls changes the water circulation pattern near them and, consequently, affects larval settlement; in this case, it probably increases the chance of larvae survival long enough for them to settle.

Dendropoma corrodens exploits a habitat whose environmental conditions vary little throughout the year. As reported by HADFIELD *et al.* (1972) for *Dendropoma meroclista* and *Dendropoma rhyssconcha*, and by HUGHES (1979) for *Dendropoma corallinaceum*, this genus preferentially colonizes patches of the coralline alga *Lithothamnium*. Dispersal seems to be very low, and the settlement of several juveniles around a female has been observed, even when the juveniles have the capacity to crawl to surrounding substrates.

There is evidence that both *Vermetus* sp. and *Dendro-*

poma corrodens reproduce throughout the year, apparently at the same intensity. As in the Hawaiian vermetids (HADFIELD *et al.*, 1972; HOPPER, 1981) and in specimens of *Petaloconchus montereyensis* from Monterey Bay, California, and San Juan Island, Washington, the females we collected had brooding eggs and embryos in every month, and the monthly gonad histological analysis showed growing and mature oocytes in the same individual. This indicates that females have the capacity to produce eggs constantly, and because the egg capsules are brooded in the mantle cavity, different stages of embryonic development are found at the same time in each female. HADFIELD (1989) also found in female specimens of *Petaloconchus montereyensis* a variety of developmental stages, ranging from uncleaved ova to ready-to-hatch juveniles within a single brood.

The different colors observed in the older-shelled juveniles of *Dendropoma corrodens* have been observed also by HADFIELD *et al.* (1972) in *D. gregaria*, but in a different proportion. In *D. corallinaceum*, the embryo develops a dark brown protoconch (HUGHES, 1978a).

As observed in Tables 1 and 2, the diameter of the egg capsule increases in both species from the first to the last stages as does the egg capsule volume. This increase is probably due to an increase in permeability to water; in *Vermetus* sp. the egg capsule breaks easily in the last stage, for example even when the female retracts suddenly in the shell. In *Dendropoma corrodens*, there are marked differences in the egg capsule volume between stages II and III, with no difference between I and II, or between III and IV. This is probably because the highest growth of the embryos occurs within stages II and III, when the larval shell begins to form.

Comparison of some reproductive habits of *Vermetus* sp. and *Dendropoma corrodens* with other species of these two genera that have been studied is presented in Table 3. The pattern of reproduction of *Vermetus* sp. is very similar to that of *Vermetus alli* (HADFIELD *et al.*, 1972; HOPPER, 1981), that is, in the brooding type, number of egg capsules per female, number of eggs per capsule, size of egg and larvae, and indirect development to veliger larvae. *Dendropoma corrodens*, as well as the other species of *Dendropoma* studied (HUGHES, 1978a; HADFIELD *et al.*, 1972; HOPPER, 1981), broods few egg capsules per female, and it has a relatively small egg diameter (0.276 mm) compared with the rest of the genera (*D. maximum*, 0.250 mm [HUGHES & LEWIS, 1974] and *D. meroclista*, 0.277 mm [HADFIELD *et al.*, 1972]). The protoconch size (0.512 ± 0.059 mm) in *D. corrodens* is comparable to that of other species of *Dendropoma*—*D. maximum*, 0.03 mm (HUGHES & LEWIS, 1974) and *D. corallinaceum*, 0.97 mm (HUGHES, 1978a).

Usually in *Vermetus* and *Dendropoma* species, capsules are brooded in a slit of the mantle (Table 3); see *V. alli*, *D. gregaria*, *D. platypus*, *D. ryssconcha*, and *D. psarocephala* as reported by HADFIELD *et al.* (1972) and *D. corallinaceum* as reported by HUGHES (1978a). Exceptions to the rule

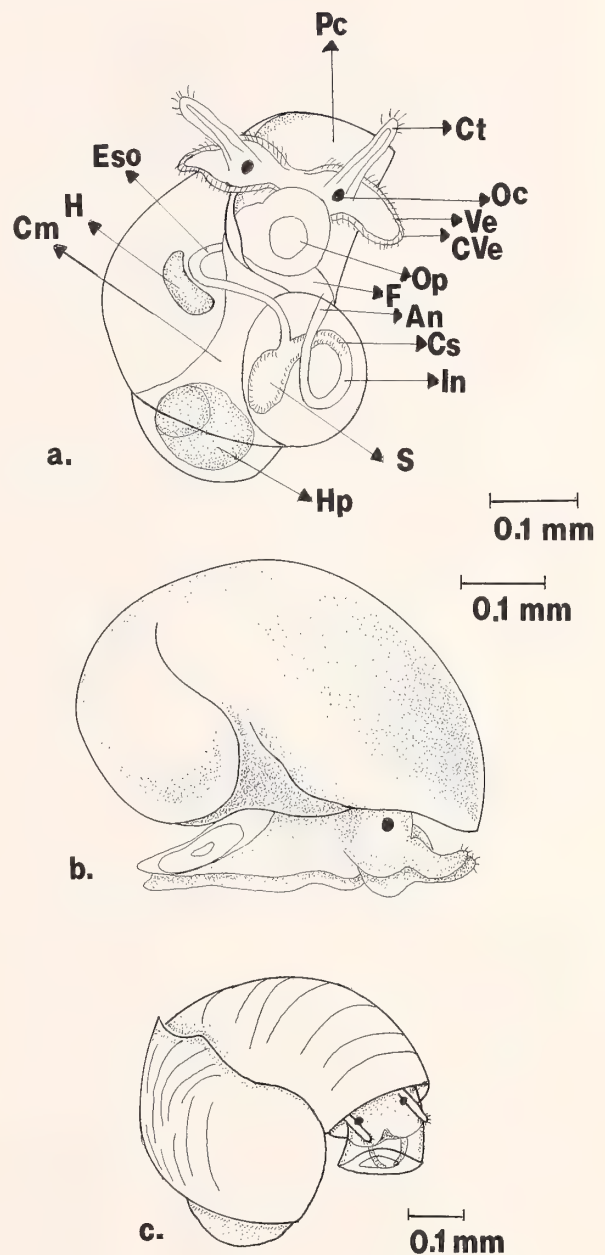


Figure 5

Dendropoma corrodens. a. Veliger larvae, stage III. b. Crawling juvenile at hatching. c. Juvenile, having fixed to the substrate. See Figure 4 for key to abbreviations.

are *D. meroclista*, *D. cf. meroclista*, *D. maximum*, and *V. triqueter*, which brood their egg capsules attached to the shell (HADFIELD *et al.*, 1972; SAFRIEL & HADFIELD, 1988; HUGHES & LEWIS, 1974; MORTON, 1965, respectively). The species of the genera *Petaloconchus* and *Serpulorbis* usually brood their capsules attached to the internal side of the shell: *P. keenae* and *S. variabilis* (HADFIELD *et al.*, 1972, *S. aureus* (HUGHES, 1978b), *S. natalensis* (HUGHES,

Table 3
Summary of reproductive aspects in the vermetid family (Lv = larvae).

Species†	Egg diameter (mm)	Embryos per capsule	Capsules per female	Brooding type	Hatching	Additional intracapsule nutrition	Reference
<i>D. corallinaceum</i>	—	1	11	mantle slit	crawling	—	HUGHES, 1978a
<i>D. corrodens</i>	0.276	8 (6–7 Lv)	1–8	mantle slit	crawling	1 nurse egg	present study
<i>D. greggia</i>	0.310	10 (6–21)	3–4	mantle slit	crawling	vesicular yolk	HADFIELD <i>et al.</i> , 1972
<i>D. maximum</i>	0.250	311–444	15	shell	crawling	not observed	HUGHES & LEWIS, 1974
<i>D. meroclista</i>	0.277	3–16	6	shell	crawling/late veliger	yolk?	HADFIELD <i>et al.</i> , 1972
<i>D. cf. meroclista</i>	0.130	21–134	2–6	shell	veliger	—	SAFRIEL & HADFIELD, 1988
<i>D. platypus</i>	0.350	70	5	mantle slit	crawling	vesicular yolk	HADFIELD <i>et al.</i> , 1972
<i>D. psarocephala</i>	0.300	9–23	5	mantle slit	crawling	vesicular yolk	HADFIELD <i>et al.</i> , 1972
<i>D. rhyssocoacha</i>	0.315	6–25	6	mantle slit	crawling	vesicular yolk	HADFIELD <i>et al.</i> , 1972
<i>P. erectus</i>	—	>100	—	shell	veliconchae	—	BANDEL, 1975b, 1976
<i>P. keenae</i>	0.217	130–184 (17–30 Lv)	—	shell	crawling/veliger	nurse eggs	HADFIELD <i>et al.</i> , 1972
<i>P. mcgintyi</i>	—	80–100	3–4	shell	veliger	—	BANDEL, 1976
<i>P. montereyensis</i>	0.112	372 (1 juvenile)	14.88	mantle slit	crawling	nurse eggs	HADFIELD, 1970, 1989
(San Juan Island)							HADFIELD & IAEA, 1989
<i>P. montereyensis</i>	0.110	233 (1 juvenile)	17.05	mantle slit	crawling	nurse eggs	HADFIELD, 1989
(Monterey)							HADFIELD & IAEA, 1989
<i>S. aotearoicus</i>	—	10	—	—	crawling	—	MORTON, 1951
<i>S. aureus</i>	—	30	20	shell	crawling	—	HUGHES, 1978b
<i>S. imbricata</i>	—	70–80	20–30	—	veliger	few yolk	MORTON, 1951
<i>S. natalensis</i>	—	24 (15–41)	30	shell	crawling	nutritive cells	HUGHES, 1978a
<i>S. variabilis</i>	0.190	240	48	shell	veliger	nurse eggs	HADFIELD <i>et al.</i> , 1972
<i>V. alii</i>	0.225	80–200	50	mantle slit	veliger	—	HADFIELD <i>et al.</i> , 1972
<i>V. triquetra</i>	—	85–115	4–6	shell	crawling/veliconchae	—	MORTON, 1965
<i>Vermetus</i> sp.	0.240	289 (188 Lv)	21 (1–54)	mantle slit	veliger	100 nurse eggs	BANDEL, 1975b
							present study

† *D.* = *Dendropoma*; *P.* = *Petalochonchus*; *S.* = *Serpulorbis*; *V.* = *Vermetus*.

1978a), *S. daidai* and *S. medusae* (SCHEUWIMMER & NISHIWAKI, 1982), and *P. varians* (personal observation). An exception would be *P. montereyensis*, which broods the egg capsules in a slit of the mantle (HADFIELD, 1970, 1989).

Usually, *Dendropoma* species brood many fewer egg capsules than do *Vermetus* species; *D. corrodens* broods from 1 to 8 capsules, 3 to 4 being the most common, as in *D. gregaria*. The maximum number of capsules per female reported for this genus is 15, for *D. maximum*. Both *Vermetus* species, *V. alli* and *Vermetus* sp., brood up to 50 and 54 capsules, respectively; but *V. alli* produces a few large broods per year (HOPPER, 1981) and in *Vermetus* sp. there is a continuous production of egg capsules throughout the year. In contrast, *V. triqueter* broods few egg capsules, between 4 and 6 (BANDEL, 1975b). As noted in Table 3, the egg capsules also differ in the number of embryos they contain according to the genus. *Dendropoma* species usually have few embryos per capsule (between 1 and 25), with the exceptions of *D. platypus*, which has up to 70 embryos (HADFIELD *et al.*, 1972) and produces a few large broods per year (HOPPER, 1981), and *D. maximum*, which has up to 444 embryos (HUGHES & LEWIS, 1974). Among *Vermetus* species, the range is between 80 and 289 embryos per capsule. At hatching, all the *Dendropoma* species studied are crawling juveniles with the exception of *D. merochlista*, which presents the two hatching modes: crawling juveniles and late veliger larvae (HADFIELD *et al.*, 1972). However, the *D. cf. merochlista* found on the Sinai coasts of the Gulf of Elat hatches as a typical planktonic veliger larva (SAFRIEL & HADFIELD, 1988). Both *Vermetus* sp. and *V. alli* hatch as veliger larvae, and *V. triqueter* may hatch as a veliconch larva or as a crawling juvenile (BANDEL, 1976).

Additional nutrition during embryonic development has previously been reported in other species of the family by MORTON (1951) in *Serpulorbis imbricata*, by HUGHES (1978a) in *S. natalensis*, and by HADFIELD *et al.* (1972) and HOPPER (1981) in *Dendropoma gregaria*, *D. merochlista*, *D. platypus*, *D. rhyssconcha*, *D. psarocephala*, *Petalonchus keenae*, and *Serpulorbis variabilis*. Of special interest is the case of *P. montereyensis*, in which each capsule typically produces only a single embryo, with the remainder of the 164–499 eggs in a capsule serving as nurse yolk for the one developing embryo (HADFIELD, 1989; HADFIELD & IAEA, 1989).

Both *Vermetus* sp. and *Dendropoma corrodens* ingest nurse eggs but in two very different ways. In egg capsules of *Vermetus* sp., the nurse eggs (about 100 for the development of 200 veliger larvae) remain inside the egg capsule as a compact mass, until they are almost completely consumed by the embryos at the time of hatching. In egg capsules of *D. corrodens*, one nurse egg provides additional nutrition to the six or seven embryos, and its disintegration into yolk particles occurs within the first hours of development, that is, after the start of stage I and before stage II; a similar phenomenon was described by PENCHASZADEH (1976) for two species of the genus *Trophon*.

ACKNOWLEDGMENTS

We thank Dr. Rudiger Bieler of the Delaware Natural History Museum, who spent a couple of weeks with us in February 1986, for helping us with the identification of the species and for reviewing the manuscript, improving this paper with useful comments. We are especially grateful to Eduardo Klein for one year of help on the field trips and the statistical treatment of the data, and to Dr. David Bone of the Universidad Simón Bolívar for reviewing the manuscript. We are indebted to INTECMAR and CONICIT, Venezuela, for financial support.

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BOOKS, PERIODICALS & PAMPHLETS

Systematic Revision and Suprageneric Classification of Trochacean Gastropods

by CAROLE S. HICKMAN & JAMES H. MCLEAN. 1990. Natural History Museum of Los Angeles County, Science Series No. 35. 169 pp., 100 figs.

The order Archaeogastropoda occupies a distinguished, if unappreciated, position in the evolution of life. From small, inconspicuous, Lower Cambrian beginnings, it has survived the vicissitudes of a half billion years of earth history. And its cladogenetic proclivities generated the most spectacular evolutionary radiations in the Mollusca, producing the remarkably successful opisthobranch and pulmonate subclasses as well as the diverse and more accomplished caenogastropods within the Prosobranchia.

The goal of this monograph was improvement of the family-group level classification of a major and pivotal superfamily of archaogastropods, the Trochacea (the authors eschew the more current form, Trochoidea). It results from lengthy and diligent efforts of the most knowledgeable contemporary systematists of the group, it reports a great deal of original research and substantial progress in understanding the taxon, and it succeeds in presenting a richly illustrated, more rational classification, new appreciation of the diversity of trochacean structures and life styles, and a provocative phylogenetic hypothesis.

The authors present their systematic approach as “concept and objectives,” worth summarizing as their ten commandments for revisionary taxonomy. Thou shalt: 1, clearly diagnose higher taxa; 2, base diagnoses on apomorphies rather than collections of plesiomorphies; 3, construct large character sets with clearly defined character states; 4, use only characters scored for all taxa; 5, avoid proliferation of higher taxa; 6, provide standardized comparative illustrations of all character sets for all taxa; 7, include the fossil record and stratigraphic age as evidence of evolutionary history; 8, summarize biogeographic and ecological data for each taxon; 9, use natural history data in systematics; 10, identify currently unresolved problems and promising topics for future research.

The monograph clearly reflects adherence to these policies. That it was a formidable task is evident at the outset because, by outgroup comparison with Pleurotomariacea, the major apomorphies of the Trochacea are negative, that is losses of characters: “The most important innovations of Trochacea include loss of the shell slit, labral emargination, or tremata and loss of the right ctenidium.”

In the evolution of prosobranchs, as in primates, the tales of teeth are telling. Probably the most important contribution of this work is its development and synthesis of extensive, largely original comparative data on trocha-

cean radular patterns. The radula is a very complex structure as well as a major evolutionary innovation of the Mollusca. As in mammals, the numbers and types of teeth, their independent and interdependent modifications, and their positional and functional relationships to each other afford a rich set of characters and states. The authors have discovered many of these, and they illustrate them with the results of excellent SEM studies and a few “in your face” views of radulas at work as well. The table of trochacean radular attributes lists an impressive 47 characters, with essentially all states coded as binary.

Radular characters are weighted most heavily and described in greatest detail. A morphological overview section only introduces the topic; most of the basic comparative and functional morphology is in the systematic treatments. Radulas are quite constant in the Turbinidae, so other characters must be used in this family, but the evolution of Trochidae involved several interesting trends, often in the directions of reduced number of teeth per row and specialization of those remaining.

The table of non-radular characters contains 71 entries pertaining to shell (26), foot and epipodium (17), operculum (9), snout (9), ctenidium (6), eyestalks, and buccal cavity. The overview section discusses some of these cogently and illustrates them well, *e.g.*, epipodial features and radial and tangential shell aperture orientations and their biomechanical significance. Others get shorter shrift, *e.g.*, the “pseudoproboscis,” operculum secretory region, and ctenidial afferent membrane. The character states of the latter two are given only as long or short, that is they are treated as binary characters although their variation is surely continuous. More explanation would have been particularly welcome here, as these are important characters at the subfamily level and subfamilies are particularly important in this monograph. While retaining the familiar Turbinidae and Trochidae as the only major families of Trochacea, Hickman and McLean accommodate their new taxonomic results primarily by establishing a number of new subfamilies.

The authors’ taxonomic approach draws both from evolutionary systematics and cladistics. Their methodology seeks to take advantage of the positive contributions of cladistics (reliance on shared, derived characters, objectivity, precision, reproducibility of results, and testability of phylogenetic hypotheses) while avoiding the shortcomings (nonrepresentation of anagenetic change and degree of divergence, reliance on parsimony, and difficulties with accommodating continuously varying characters and both contemporaneous information and the fossil record).

This methodology will irk advocates of purity (that is, cladistics or evolutionary phylogeny or phenetics but please not a mix), or who follow commandments of other gods

in theoretically framing systematics research, and it will frustrate users who would like the evidence up front, before the interpretation. Here, characters and states are presented, their polarities, apomorphies and convergences asserted, and they are used to develop the classification, sometimes with limited defense. Character state polarities are congenitally if concisely argued at the family level, but as noted above the authors' main taxonomic innovation is the establishment of numerous subfamilies. The reader is not given explicit evidence supporting, for example, absence of cephalic lappets in Solariellinae as a secondary loss rather than plesiomorphic, small size as secondary in Coloniinae, or four pairs of epipodial tentacles as primitive to three pairs.

The monograph concludes with a brief but densely packed summary containing diagrams that look suspiciously like cladograms or trees—at least taxa are the terminal buds of a hierarchical branching pattern. However, these are based on and summarize the classifications and their diagnoses presented in the main text. They are not cladograms in the usual sense, in which state differences in the selected character sets are allowed to generate tree topologies. The authors characterize the results of such usual cladistic analyses as “analytical cladograms.” They distinguish the diagrams they present rather as “retrospective cladograms,” that is they are derived *a posteriori* from the classification.

This reviewer is inexpert in both Trochacea and cla-

distics. The former have made only a few cameo appearances in his papers, and he has published only one modest cladistic analysis (and that a decade ago), and last year subtitled a seminar “Why not to be a cladist” (after VAN VALEN, 1978). But he is a bit uneasy that this volume does not give cladistics a fair shake at the problem addressed. Modern computer packages accommodate character weighting (*e.g.*, SANDERSON, 1990), and the authors' treatment of quantitative characters, while questioned above, is suitable for cladistic analysis. One would like to see what alternative trees a cladistic treatment would generate from the characters and states carefully presented, and the likelihoods of the trees presented here under cladistic constraints. However, I suspect that Hickman and McLean's intimate knowledge of the biology and paleontology of trochacean gastropods, and their explicit methodology and presentation of output from the highly effective supercomputers for systematics in their minds, bring us closer to knowing the true phylogenetic history of the Trochacea.

Alan J. Kohn

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NOTES, INFORMATION & NEWS

First International Latin American Malacological Congress Caracas, Venezuela, 15-18 July 1991 Proposed North-South Collaboration

We have recently returned from participating in this important and precedent-setting meeting. The purpose of this memorandum is to convey some of our impressions, and to advance some proposals for future collaboration between malacologists in Latin America and those of us in the United States, Europe, and elsewhere.

This Congress was a long time in coming. Plans were first advanced for a Latin American meeting in Costa Rica in 1984, but these never materialized. A second attempt, in Colombia in 1986, was also unsuccessful. Finally, the right set of factors came together—financing, institutional support, and organizational abilities—to bring about the Congress held in Caracas this past July. A great deal of credit goes to Dr. Paulo Penchaszadeh of the Universidad Simón Bolívar, site of the Congress, but especially to Robert Cipriani, who devoted much of his time over several months to organizing the event.

Participants stayed in hotels in downtown Caracas, traveling by bus each day to the Universidad Simón Bolívar, which nestles in a mountain valley about 1300 m elevation, some 30 minutes from the center of the city. A final banquet was held in a fine restaurant in downtown Caracas.

The Congress was a great success, beyond any of our expectations! It was attended by some 170 participants and other malacologists and students from most countries in Latin America and the Caribbean. Particularly well represented were, of course, Venezuela, but also Mexico, Brazil, and Chile. Other Latin American countries represented were Peru, Costa Rica, Argentina, Panama, Cuba, Bolivia, Saint Lucia, Martinique, and Turks. Other attendees were present from the United States, including Puerto Rico, Spain, The Netherlands, Italy, and Great Britain. Approximately 90 papers and 9 posters were presented featuring land, freshwater, and marine mollusks, and including paleontology.

In part, the Congress attracted so many malacologists and students because of a symposium on *Strombus gigas* organized by Richard Appeldoorn of the University of Puerto Rico. Fishery for this commercially important species is on the decline throughout the Caribbean, and symposium participants were able to share information on the biology of this species and on measures that can be taken to achieve a more sustainable fishery.

A new display of mollusks in the Natural History Museum of the Universidad Simón Bolívar was unveiled at the meeting, featuring displays of Venezuelan mollusks, both Recent and fossil.

What of future Congresses? Malacological leaders present at this Congress concluded that a Latin American association with officers and individual members would not be practical at this time and would be difficult to sustain. Instead, they agreed on, and formed a loose-knit steering committee working with a few participants from each country who would serve as points of information exchange to institutions and amateur groups in their countries.

The steering committee, called the Comité Organizador de Congresos Latinoamericanos de Malacología, was formed 18 July 1991, and consists of:

M. Sc. Martha Reguero Reza, Presidente (México)
Dr. Antonio García Cubas, Vicepresidente (México)
Dra. María Villarroel Melo, Secretaria (México)
Dr. José Willibaldo Thomé, Vocal de Programa (Brazil)
Dr. Paulo E. Penchaszadeh, Vocal de Programa (Venezuela)
Lic. Roberto Cipriani Fita, Vocal de Programa (Venezuela)

The functions of the committee are to: (a) assure the continuity of periodic meetings; (b) establish contact with an advisory group formed by the presidents of the various malacological societies existing in Latin America; (c) promote the establishment of regional malacological societies in those countries where they do not exist, developing lists of malacologists in each area; and (d) approve the frequency and sites of congresses, and the constitution of the local organizing committees, with a view to bringing about future meetings.

A second congress will be organized in two or three years, probably in Mexico. The Comité suggested that it might be appropriate to consider joint meetings in a few years with the American Malacological Union, the National Shellfisheries Association, and eventually hosting with *Unitas Malacologica*.

Meanwhile, other measures are necessary to further the progress of malacology in Latin America and the Caribbean. There is especial need for enhancing communications with workers with common interests and providing access to literature and materials in these countries. These malacologists, though having great enthusiasm and ability, meet with considerable frustration because of inadequate resources.

A number of proposals were advanced by the Comité. For example, the kinds of workshops that Brian Morton and others have run in Hong Kong and elsewhere allow more intensive interaction with skilled professionals. With a little advance planning, visitors can give "short courses" on specific topics and, in most cases, these need not be in

Spanish. Resulting in significant benefits would be some major collaborative projects on particular topics among a number of workers with different skills in different countries; the classification of a particular family, such as the oysters, or the biology of a gastropod like *Strombus*, are possible examples.

The key problem is, of course, resources. While that problem is significant for institutions in the United States, it is acute in Latin America and the Caribbean, where universities with a number of students and faculty interested in malacology lack key literature on the subject. Surely we can do more to help!

One final major proposal emerged from the Comité meetings: to form semi-formal, north-south sister institutional linkages. Scientists in the United States and elsewhere have been very helpful and generous to individual Latin American and Caribbean scientists making specific requests of them for literature or other help. However, this has been very episodic, and our southern colleagues are often unaware of the resources they need or persons with whom they should be in contact. It thus occurred to us that semi-formal matching, or linking, of key institutions could result in meaningful mutual benefits.

More specifically, we are thinking of taking steps to link one United States institution, such the malacology department of a museum or university, with one or two centers of malacological activity in Latin America or the Caribbean. The United States institution would, at a minimum, provide a point of first communication for the southern institution(s) by suggesting to them literature, persons, or other resources. In return, the Latin American institution would serve the same function for work going on in its area. Beyond this, and at the discretion of the institutions involved, would be exchanging literature, trading literature for specimens needed in northern institutions for research, reciprocal visits, joint projects, and the like.

The Comité Organizador de Congresos Latinoamericanos de Malacología is undertaking a country-by-country survey of needs and which institutions might be most appropriate for such linkages. In return, we have agreed to make such a survey in the United States, and Henry Coomans of The Netherlands and Andy Beaumont of Great Britain, who attended the Congress, will make similar inquiries in Europe.

So, we end with the important question: Would your institution be willing to serve as a contact point for Latin American and Caribbean exchanges? Have you an interest in a particular country or institution? Please drop us a note, mailing it to Gene Coan.

Dr. Gene Coan
891 San Jude Ave.
Palo Alto, California 94306

Dr. Melbourne R. Carriker
College of Marine Studies
University of Delaware
Lewes, Delaware 19958

Dr. Donald R. Moore
RSMAS, University of Miami
4600 Rickenbacker Causeway
Miami, Florida 33149

V Reunion Nacional de Malacología y Conchiliología [Fifth Mexican Malacological Congress]

Once again we have the opportunity to meet to learn about advances in investigations in malacology, conchology, and related fields. This time the meeting will be in the colonial city of Morelia, which the hosts would also like to show you. They want to surprise you!

The Universidad Michoacana de San Nicolás de Hidalgo and the Sociedad Mexicana de Malacología will have a large place for the meeting in the Museo Michoacano for the event, which will occur between the 8th and 12th of December 1992.

The organizing committee for the meeting includes Dra. María Villarroel and Biol. Ezequiel Gónzáles of the Universidad Michoacana, and Dra. Martha Rugero and Dr. Antonio García Cubas, of the Universidad de México.

Abstracts are due before 14 March 1992, and full papers before 18 July 1992. The correct form for abstracts and full papers will be the same as for the Fourth Congress. Instructions will be sent with the second notice, together with information about the program and all the information necessary to begin to plan your trip to Morelia.

For more information, write to Dra. Villarroel at the Universidad Michoacana, Apdo. Postal 59-3, C.P. 58021, Morelia, Michoacán, México.

Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, *not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete, with all journal titles *unabbreviated*, and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *The Veliger* 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

Tables

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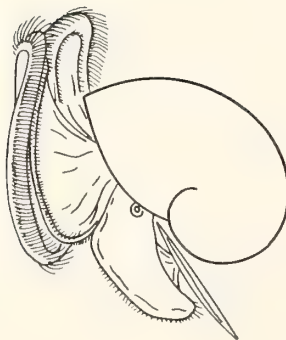
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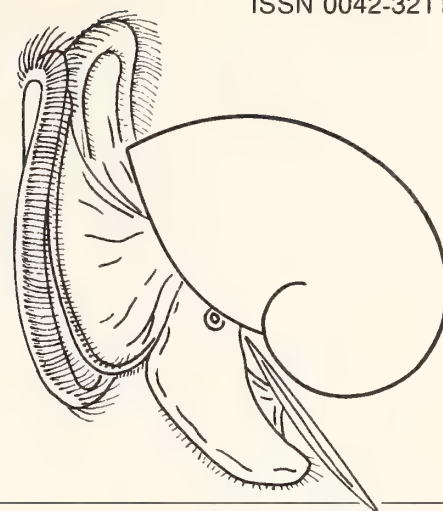
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Anterior Inhalant Currents and Pedal Feeding in Bivalves

by

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Abstract. The association of anterior inhalant currents and pedal feeding is examined in four bivalve species: *Corbicula fluminea*, *Mysella bidentata*, *Tridacna gigas*, and *Patinopecten yessoensis*. At some time in the life cycle they all employ the foot for food particle collection. In *Corbicula* and *Mysella* this is an adult activity, but in *Tridacna* and *Patinopecten* the behavior is confined to the early juvenile. The position of the inhalant current is determined by the dominant food collecting organ. We argue that pedal feeding is a primitive bivalve function. Where the habit is confined to the early postmetamorphic stage, the use of the foot as a feeding organ spans the period between larval and late juvenile suspension feeding before the gills develop into effective filtration organs. It is probable that this kind of feeding behavior is almost universal in juvenile bivalves and common in the adult forms of small species. This has some importance for bivalve aquaculturists in view of high postmetamorphic mortalities in cultured bivalves that may result from inappropriate feeding regimes.

INTRODUCTION

The anterior inhalant current found in Protobranchia such as Nuculidae and Solemyidae has long been considered a primitive condition (YONGE, 1939). It is also found universally in the Lucinacea (ALLEN, 1958), and in some minute species belonging to the Galeommatacea (= Lep-tonacea), and Veneracea (OLDFIELD, 1955). OCKELMANN & MUUS (1978) suggest that in small bivalves, especially juveniles, the anterior inhalant current is the answer to the functional problem of separating the inhalant from the exhalant currents. They note, "No exception is known to the rule that this flow pattern is found in all bivalve species at least for a time in postmetamorphical life." Descriptions of such currents are provided by ALLEN (1961) for *Pandora inaequalis* (Pandoridae), by MORTIMER (1962) for three *Nucula* spp. (Protobranchia: Nuculidae), by CADDY (1969) for *Macoma balthica* (Tellinidae), by BAYNE (1971) for *Mytilus edulis* (Mytilidae), by AABEL (1983) for *Abra alba* (Semelidae), and by KING (1986) for *Panope abrupta* (Saxicavidae). Thus the potential for acquiring food through an anterior aperture is general amongst juvenile and small bivalves. The particular aspect that we address here is the association of an anterior inhalant current with the actions of the foot and labial palps, to constitute a feeding habit

distinct from suspension feeding and deposit feeding modes involving the posterior inhalant siphon and ctenidial filtration.

In the lucinacean *Fimbria fimbriata*, the pedal cilia draw an anterior feeding current from the water column through a thin layer of substrate (MORTON, 1979). When the large foot in this species is protracted into the substrate, its cilia collect deposit particles that enter the mantle cavity and pass them to the ventral marginal food grooves of the gills. When the foot is retracted, its coating of mucus-bound particles is wiped off by the secondarily developed pallial palps, the true palps being vestigial. MORTON (1980) also postulates that the anomalodesmacean *Pholadomya candida* (Pholadomyidae) uses the foot as a pump for drawing fine sediment and detritus into the mantle cavity. While MITROPOLSKIJ (1966) reports particle collection by the foot of the fresh-water sphaeracean *Pisidium casertanum*, LOPEZ & HOLOPAINEN (1987) state that the particles adhering to the foot are all removed as pseudofeces. Nevertheless, the "interstitial suspension-feeding habit" of *Pisidium* reported by the latter authors is of some interest in the present context. The intertidal bivalve *Geloina erosa* may fit this category since MORTON (1976) has demonstrated that at low tide it draws burrow water into the mantle cavity through the pedal gape and ingests particles from it.

BERNARD (1974) notes that in preserved specimens of the carnivorous Cuspidariidae the tip of the foot is often found inserted into the mouth, and he infers that the live prey, once inside the mantle cavity, are ingested with the aid of the foot.

Hitherto, these isolated cases were the only known examples of direct nutritional functions of the foot in mature bivalves. However, there are indications of such a role in some studies of juvenile bivalves. ALLEN (1961) observes that the combined use of the ciliated tip of the foot and the relatively large labial palps produce respiratory, cleansing, and feeding currents. MORTIMER (1962) notes particulate food collection by the ciliated foot of early post-metamorphic juveniles of several *Nucula* spp. BAYNE (1971) observes that the ciliation of the foot in juvenile *Mytilus edulis* creates an active feeding current that brings food particles into contact with the inner surfaces of the labial palps. At this stage the gills are not sufficiently developed to create a posterior inhalant current or to collect and pass food to the mouth. CADDY (1969) finds that the pedal ciliation has a similar role in juvenile *Macoma balthica* (Tellinidae). AABEL (1983) points out that when the foot of juvenile *Abra alba* contracts during the "digging cycle," adhering particles are brought into the mantle cavity, along with a sudden influx of water and suspended particles.

A definitive study by KING (1986) of juveniles of the geoduck *Panope abrupta* (Saxicavidae = Hiatellidae) reveals the full significance of pedal feeding. After metamorphosis at 4 weeks *Panope* juveniles use "pedal-palp feeding" exclusively through 6 weeks of byssal plantigrade development, and this feeding mode continues to some extent until deep-burrowing behavior is established about 12 weeks after metamorphosis. The juvenile lies on its side, extends the foot posteriorly, and then sweeps it anteriorly. Deposit material and mineral particles are bound by mucus and carried adorally by pedal cilia. When the foot reaches the limit of its anterior extension it contracts; the mucus-bound particles are loosened and formed into a bolus by the vortex created by the cilia of the inner faces of the labial palps. Passive contact between the labial palps and the base of the foot, and muscular flicking motions of the palps also free the mucus-bound particles. Occasionally the foot is reflexed and the propodium stuffs the food bolus into the esophagus. This food collecting behavior is stereotyped and distinct from digging. If there is no suitable food or substrate, the animals locomote for prolonged periods. Pedal-palp feeding fills the nutritional gap between the suspension feeding mode of the veliger and the suspension feeding mode of the adult. Five weeks after metamorphosis the gill bars extend and reflex, forming a ciliated food groove at their ventral tips, and at this stage they are able to create a weak posterior inhalant current. However, there is still no functional connection between the gills and the mouth, and the posterior current is disrupted by the large foot. Not until 12 weeks after metamorphosis are the gills sufficiently large to filter efficiently,

by which time they are functionally connected, via food grooves, with the mouth.

The use of oysters as type models for bivalve studies has probably been responsible for the general assumption that the bivalve veliger suspension feeding mode is immediately replaced by the adult filter feeding mode. Oysters rapidly develop functional gills within a day of settlement and attachment. Boring bivalves such as the Terebinidae and Pholadidae develop inhalant siphons at the pediveliger stage and rapidly engage in the mature feeding mode as soon as they form their burrows (WERNER, 1939; JORGENSEN, 1946; TURNER & JOHNSON, 1969; CULLINEY & TURNER, 1976). However, there are enough hints in the literature cited above to conclude that the pedal-palp feeding behavior of *Panope* juveniles is widespread, and that oysters and borers are exceptions to a general rule.

The present report discusses four cases of pedal feeding in bivalves. The first is in *Corbicula fluminea* (Corbiculidae), a fresh-water species whose members attain 4–5 cm in shell length (McMAHON, 1983). The second is *Mysella bidentata* (Leptonidae), a marine, benthic bivalve that does not exceed 5 mm in shell length. The final two examples are the giant clam *Tridacna gigas* (Tridacnidae), and the Japanese scallop *Patinopecten yessoensis* (Pectinidae), both marine epifaunal organisms, where pedal feeding occurs only in the early juveniles. These studies were initiated independently by McMahon and Reid (*Corbicula*); Ó Foighil (*Mysella*); Reid (*Tridacna*); and Finnigan and Ó Foighil (*Patinopecten*). Thus the experimental and observational approaches vary from one species to another. We have collaborated in this joint report in order to emphasize the variety of bivalve types that exploit similar modes of pedal feeding.

MATERIALS AND METHODS

Corbicula

Specimens of *Corbicula fluminea* (Müller) were collected from the Clear Fork of the Trinity River below Benbrook Lake in Tarrant County, Texas. In preparation for feeding experiments some specimens were kept in filtered water for either 8 or 24 days. This conditioning was for the purpose of a study of the digestive cycle that will be reported elsewhere but is nevertheless relevant to our present report.

The suspension feeding mode, consisting of filtration of the inhalant siphonal current, was examined by placing the specimens in shallow pans to which cultured *Chlamydomonas reinhardtii* was added. The deposit feeding mode was examined under a variety of conditions. In the first, freshly collected detritus was thinly layered in shallow pans before the animals were introduced. In other instances the pans were thinly layered with ashed and rinsed sand and silt from the biotope and then with soaked G10 Sephadex beads. The mineral particles ranged from 10 to 600 μm in diameter and the Sephadex beads ranged from 40 to

120 μm but were mainly in the 60 to 80 μm range. *Corbicula* specimens were placed on the deposit layer, care being taken not to resuspend the Sephadex beads. Pedal feeding was also observed when *Corbicula* specimens were placed in deep gravel in narrow glass tanks. Stomach contents were examined microscopically 1–12 hr after active feeding had commenced.

Ciliary currents in the mantle cavity were examined after removal of the upper valve and mantle. Particles used included 280 mesh carborundum (35–75 μm), alumina (ca. 30 μm), and G10 Sephadex beads (40–120 μm).

Mysella

Specimens of *Mysella bidentata* (Montagu) were collected by Van Veen grab from a depth of 18 m in inner Galway Bay, Ireland. They were placed in aerated aquaria maintained at a temperature of 12°C containing a layer of the sandy mud from the biotope, and their behavior was examined through a dissecting microscope within 3 days of sampling. Some specimens fed at the surface of the sediment and others that had dug shallow burrows could be seen through the sides of the aquaria. Stomach contents were determined by histological examination of specimens fixed within 1 hr of sampling.

Tridacna

Two specimens of early juvenile *Tridacna gigas* Linné were examined at the James Cook University Giant Clam Aquaculture Project on Orpheus Island, Great Barrier Reef, Queensland. These were 1 mm and 1.4 mm in shell length and had undergone metamorphosis 6 weeks before they were examined.

The specimens were studied under two conditions. In the first case they were placed in seawater in a petri dish along with some of the deposit material from the bottom of the rearing tank. This material consisted of settled phytoplankton and flocculent organic matter that formed loose clumps, leaving most of the glass bottom of the dish exposed. The locomotion and nature of the inhalant currents were observed microscopically. In the second case a 5 mm layer of surface silt, sand, and deposit material from the lower mangrove was placed in a petri dish that was then filled with seawater. After the substrate had settled the behavior of the juveniles was observed microscopically.

Patinopecten

Spat of *Patinopecten yessoensis* (Jay) that had been newly set on kinram (a filamentous substrate used for spat collection and early development of juveniles) were supplied by the Pacific Biological Station, Nanaimo, B.C. The juveniles were between 256 μm and 272 μm in length at metamorphosis. A constant flow of seawater (9.7°C, 32‰ salinity) was filtered through 125 μm nitex and then through 25 μm nitex. Once a day the water entering the tanks was

shut off and *Chaetoceros calcitrans* and *C. gracilis* were added to the aquarium at a concentration of 40,000 cells/mL. Spat were either observed on the kinram with a dissecting microscope and a videomicrographic camera, or were removed from the kinram and placed in well slides to observe their behavior with an inverted microscope with a cool light source. Some detritus derived from the algal food, and some suspended algae, were present in the samples observed with the inverted microscope. Observations were made periodically until the juveniles had reached a size of 470 μm .

RESULTS

Corbicula

In the horizontal position in our experimental trays where the layer of particulate matter was only a few millimeters thick, the animals extended the feet horizontally, with the ventral margin somewhat recurved as shown in Figure 1a. Under these conditions only the cilia of the lower side of the foot are active in particle collection. Particles placed on the upper side of the foot are not transported. As the substrate is conveyed to the mantle cavity, the ventral margin of the foot levers the animal across the surface, with the umbones in the leading position, at rates of up to 1 cm/min. In the horizontal position pseudofeces are formed at the lower shell-mantle margins and are discarded in a mucus-bound string. Observations with Sephadex beads demonstrated that in this position deposit feeding effectively transported particles that were ultimately found in the stomach. Under the conditions of our experiments there was no resuspension of Sephadex nor uptake through the inhalant siphon. However, the route of uptake is problematical due to the presence of the pedal rejectory tract and the opacity of the shell of *Corbicula*. Some of the denser clumps of material are brushed off when they touch the edges of the valves and mantle marginal folds. Pedally collected particles that continue into the mantle cavity somehow escape rejection and either are caught up in the marginal ctenidial food grooves (some Sephadex beads are found here in dissected specimens), or are brought into direct contact with the labial palps by the contraction and forward extension of the foot. The rejectory tract may be activated only when large quantities of dense matter have built up. The trauma of dissection may activate the rejectory tract when “half-shell” animals are examined. When this is done the pedal collecting mechanism is deactivated, which may be why the mechanism has been largely overlooked in an otherwise widely observed species. Another reason might be that starved *Corbicula* may take a number of hours to begin to feed pedally.

When *Corbicula fluminea* is in a vertical position, with the foot extended down into the substrate, ciliary currents on both sides of the foot conduct particles dorsally into the mantle cavity (Figure 1b). Some of the large particles and mucus-bound clumps are brushed off on to the mantle

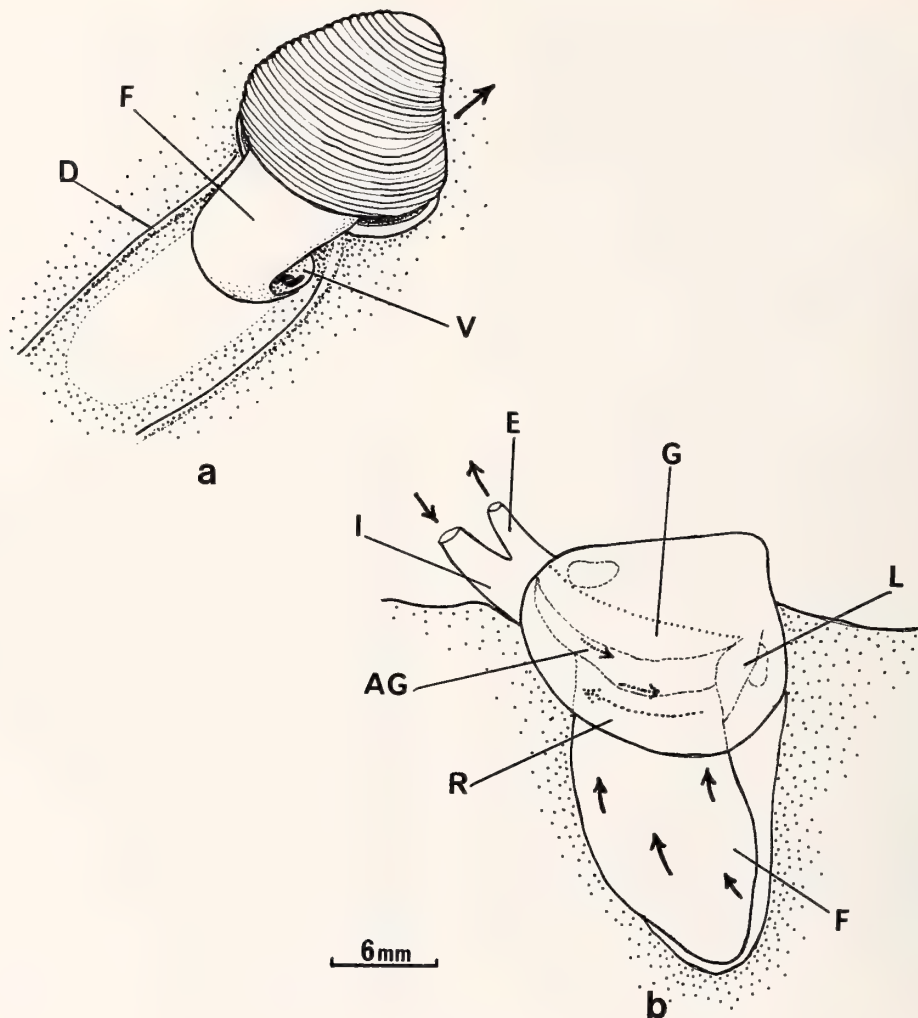


Figure 1

Pedal feeding in *Corbicula*. a. Feeding on a hard surface with a thin sand and detritus layer; large arrow indicates direction of movement of animal. b. Feeding while partially buried in sediment. AG = acceptance tract of gill food groove; D = debris displaced by advance of animal, together with mucus-bound pseudofeces; E = exhalant siphon; F = foot; G = gill; I = inhalant siphon; L = labial palp; R = rejectory groove; V = ventral pedal feeding tract.

edges, which produce more mucus that binds this rejected material into pseudofeces. These are left behind in two strings as the animal advances. Animals placed on deep sediment in laboratory aquaria locomote rapidly through the substrate for prolonged periods. In freshly collected field specimens we have repeatedly observed massive accumulations of detritus in an anterior position just below the marginal gill food grooves. We believe that these accumulations result from pedal feeding during locomotion.

In the central portion of the foot, there is a narrow anteroposterior band of ciliated grooves. When specimens were observed with the upper valve and mantle tissue removed, the foot was contracted into the mantle cavity and the anteroposterior grooves acted as a rejectory tract, carrying material towards the opening of the inhalant si-

phon (Figure 1b; see also BRITTON & MORTON, 1982). Scanning electron microscopy of the contracted foot revealed a uniform ciliation over the surface of the organ, with larger cilia near the ventral margin. The rejectory tract is furnished with ciliary tufts similar to those found in the siphons by KRAEMER (1983), who postulates that they are mechanoreceptors.

The stomachs of specimens of *Corbicula* examined within 2 hr of collection from the field contained relatively large volumes of green-brown fluid. Algal material included numerous chains and individual cells of *Nitzschia*, *Melosira*, *Scenedesmus*, and *Tabellaria* spp., which can be both benthic and planktonic, together with numerous planktonic coccoids and chlorococcum spores. Individuals of all of these algal types fall within a diameter range of

15–50 μm . Some of these algal cells were bright green, others were brown, indicating that they either had been detrital or had already been partly digested. The majority of gastric mineral particles were about 20 μm in diameter, with a few up to 100 μm . Some detrital particles, averaging 50 μm , derived from crustacean exoskeletons, were also discovered.

Mysella

The typical feeding method in *Mysella bidentata* proceeds as follows. While lying on its side at the substrate surface the animal extends the foot posteriorly to come into contact with the sediment (Figure 2a). The foot is then protracted and moved anteriorly. During this process particles of deposit matter can be seen to ascend the foot. Upon reaching the anterior limit of its extension, the foot is withdrawn. The mantle marginal folds come into contact with the foot at this point and the larger mineral particles are brushed off. Foot protraction and withdrawal are accompanied by regular valve adductions that expel pseudofeces through the exhalant siphon. During feeding a depression is excavated in the substrate by the foot; larger rejected particles are accumulated on the anteroventral valve margins and small rejected particles are deposited posterior to the exhalant opening (Figure 2b). This behavior, which we will call pedal sweep-feeding, typically lasts for about 1 min and may be repeated for periods of up to 10–15 min. Each pedal sweep-feeding cycle is punctuated by a resting period of up to 2 min. This behavior is distinct from locomotion and burrowing behavior in that the individual does not make progress through the sediment. Occasionally, during these observations, the foot could be seen, through the translucent shell, to make contact with the mobile labial palps. This could also be confirmed by removing one valve and the underlying mantle tissue. The vigorously beating cilia of the palps brush the foot, and a bolus of material builds up and can be seen rotating between the palps.

Particles of detritus also adhere to the foot during locomotion and the animal leaves much of this material behind in a pair of mucus-bound strings of rejecta. It is conceivable that some nutritive matter obtained during locomotion is conducted by the cilia of the foot and accepted by the labial palps.

The stomach contents of field-collected specimens of *Mysella bidentata* consisted largely of detritus and benthic diatoms, with a few forameniferans and flagellates. Most of the diatoms were less than 20 μm in length.

Tridacna

When placed in a petri dish with some flocculent organic debris, locomotion of juvenile *Tridacna gigas* proceeds immediately, with the anterior protrusion of the foot, and the adhesion of the ventral surface of its anterior portion to the glass (Figure 3a). Contraction of the foot then draws

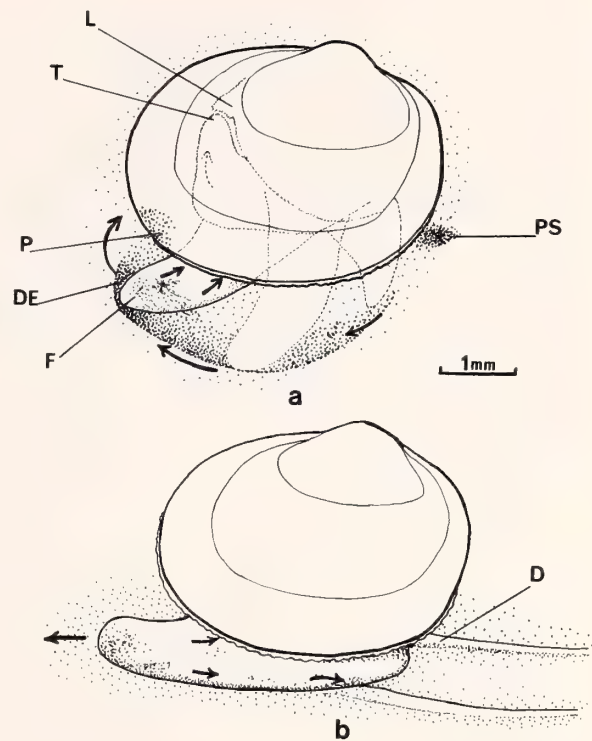


Figure 2

a. Pedal feeding in *Mysella*; large arrows indicate the posteroanterior motion of the foot. b. Locomotion and pedal currents in *Mysella*; large arrows indicate direction of movement. D = trail of material displaced by animal together with pseudofeces; DE = depression in substrate created by pedal feeding; F = foot; L = labial palp; P = particles brushed from foot adhering to valve margins; PS = pseudofeces; T = tip of foot appressed to labial palps.

the animal forward. During such locomotion an anterior current flows into the mantle cavity through the byssal-pedal gape. Small clumps of detritus are seen to enter the mantle cavity, and through the translucent valves a rotating bolus can be seen in the umbonal region, adjacent to the labial palps. On such a hard surface, locomotion continues until the organism reaches the water-air interface.

When placed in a sandy substrate with an average particle size of 100 μm , the juvenile lies on its side and engages in pedal sweep-feeding (Figure 3b). The foot is protruded posteriorly and is then swept forward with a slight rotating movement. Strings of mucus are secreted by the foot, and some, with adhering sediment particles, are shed and left behind. At the anterior limit of the foot's protraction the foot is retracted. This behavior, which lasts about 5 sec, was seen to be repeated 10 times, followed by a resting period of several minutes, after which the activity recommenced.

A second behavioral mode in sediment involves a starting position in which the juvenile is vertical with the siphonal tissues uppermost. The foot is then protruded down into

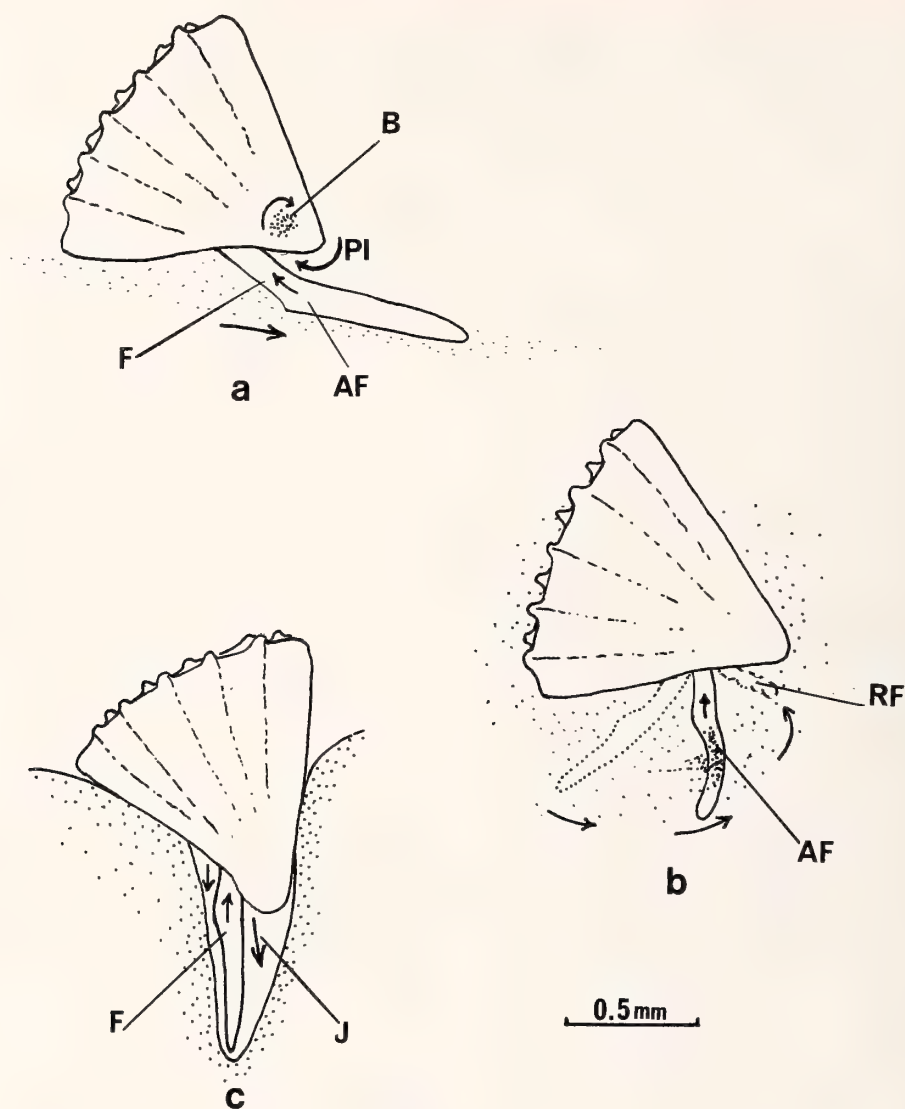


Figure 3

Various putative feeding modes of juvenile *Tridacna*. a. Particle acceptance during forward locomotion over a hard surface. b. Anteroposterior pedal feeding at substrate surface. c. Putative pedal feeding by probing substrate. AF = acceptance tract of foot; B = bolus of food particles in region of mouth; F = foot; J = jet of water created by valve adduction with siphons closed; PI = pedal inhalant current through pedal-byssal gape; RF = retracted position of foot.

the sediment (Figure 3c). Partial burrowing results from phasic adduction and the expulsion of jets of water through the byssal-pedal gape. The siphonal openings are contracted during this maneuver. It is possible that the pedal cilia gather particulate food in this mode.

Patinopecten

Newly metamorphosed juvenile *Patinopecten yessoensis* are approximately 250 μm in valve length and have 3 or 4 small, lobular primary gill filaments that increase in size

and number during subsequent ontogeny. By one week after metamorphosis the juveniles exceed 400 μm , the gill filaments become physically associated to form supra- and infrabranchial chambers and effective suspension feeding commences. Prior to this, however, if suspended food is available to the juveniles, some collection and ingestion of particles that contact the mantle surfaces does occur. Two pairs of well-developed ciliated labial palps flank the foot and are capable of passing impinging particles to the mouth.

The proportionately large foot is well ciliated on the ventral surface, and a prominent tuft of long cilia is present

at the tip of the propodium. The posterior spur or heel of the foot has a duct from which byssus can be secreted. Juveniles locomote actively by means of the foot during the first week of benthic life (Figure 4a), but the level of such activity declines as development proceeds and a more sessile, byssally attached phase ensues (Figure 5). The small juvenile protracts the foot and advances by means of the ventral cilia, the valves held vertically, with the umbones pointing in the direction of movement. In later juveniles the foot is protracted, adheres to the substrate, and then muscular contraction pulls the rest of the body forward. During both types of locomotion the foot remains extended outside the valves and is not withdrawn to contact the labial palps. The tip of the foot with its terminal tuft of cilia is very active and may have mechanosensory and chemosensory functions.

In addition to being used for locomotion and byssal attachment, the foot is used by juvenile *Patinopecten* for pedal probe-feeding. This is distinct from locomotory behavior: it does not cause forward progression of the animal. In addition, after the foot has been protracted to contact the substrate, it is withdrawn into the mantle cavity where its tip and its adhering particles are brushed against, or occasionally pushed convulsively between, the palps (Figure 4b, c). When juveniles are placed in petri dishes containing a deposit of phytoplankton, they begin to feed on this deposit using the foot in such a manner. Particles that are transferred to the palp surfaces are carried by cilia to the mouth and ingested. Several phasic adductions of the valves may occur during this process.

Observations of byssally attached juveniles on fouled kinram (Figure 5) reveal that individuals can engage in pedal-palp feeding without breaking the anchoring byssal thread. Typically the foot is progressively applied to all of the available surface through 360° of the attachment point. This is achieved by a characteristic rotational movement of the juvenile around the byssal thread, the foot being swept over portions of the substrate and withdrawn to contact the palps, before again being protracted in another direction. On occasion, byssally attached juveniles are seen to open the valves and contract the byssus retractor, bringing the labial palps into contact with the kinram. Histological examination of juveniles placed on benthic diatom mats reveal that they are capable of ingesting detrital matter and benthic diatoms (Figure 5d). Small juveniles (less than 350 μm) may feed predominantly by this method, whereas in larger juveniles (350–500 μm) the relative importance of pedal feeding, in comparison with ctenidial filtration of suspended particular food, is not clear.

In the large juveniles there are eight or more pairs of gill filaments that are partly reflexed to divide the mantle cavity into supra- and infrabranchial chambers. A ciliary flow of water enters posteroventrally and is driven by the lateral ctenidial cilia into the suprabranchial chamber and thence exits posteriorly. Suspended particles that come into contact with the gill filaments are passed dorsally and then

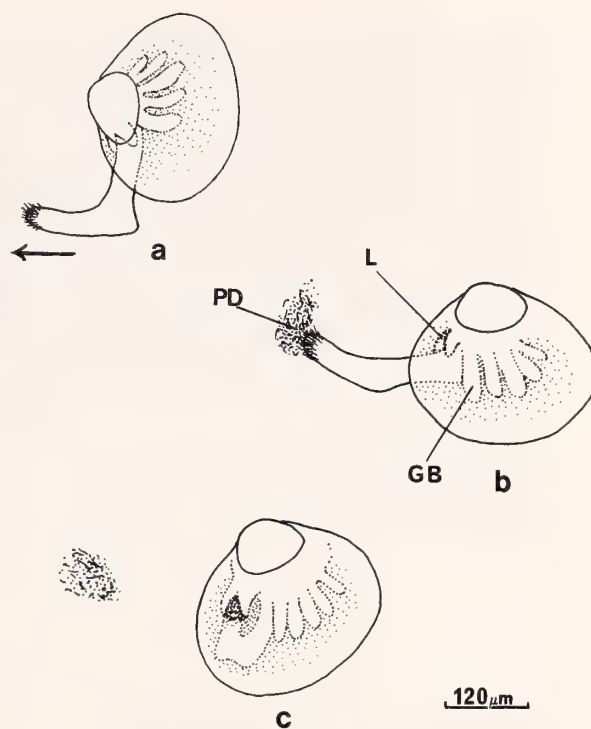


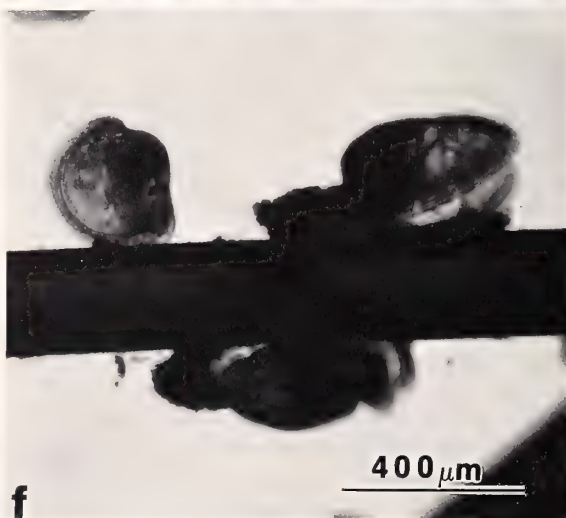
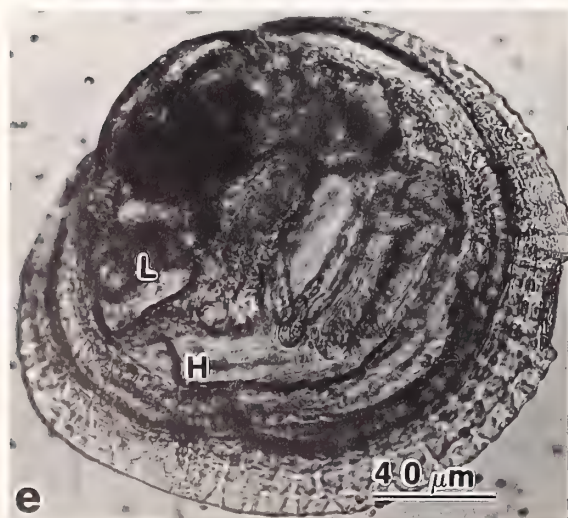
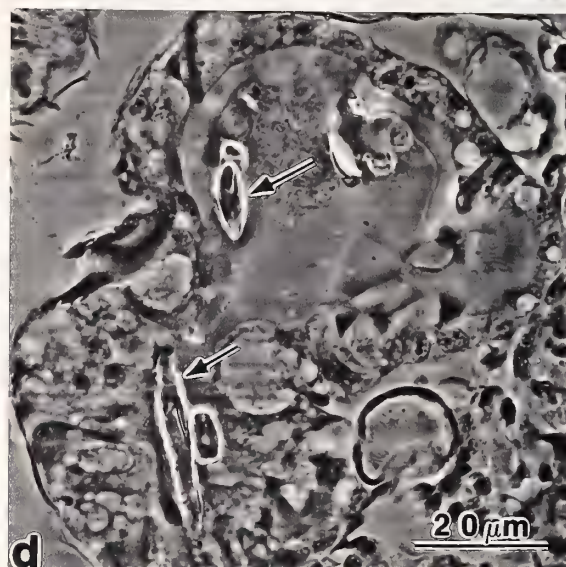
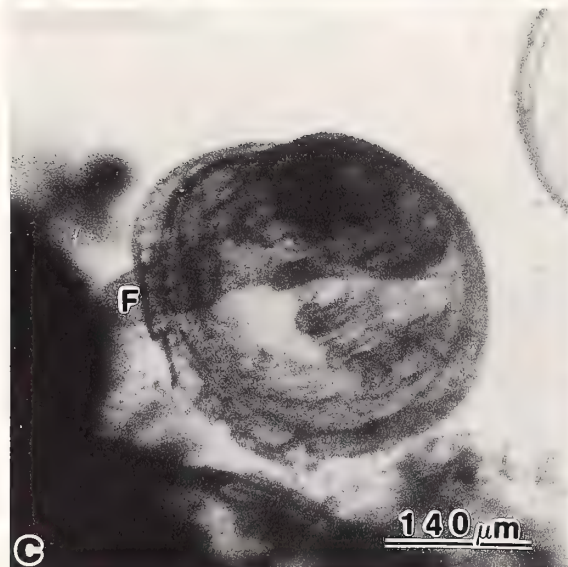
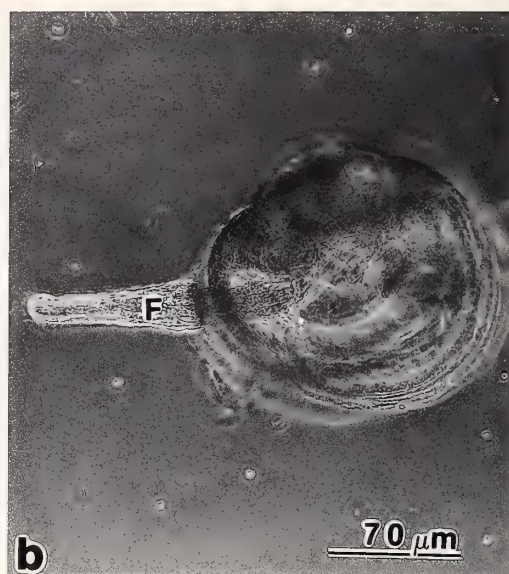
Figure 4

Early juvenile of *Patinopecten*. a. Forward pedal locomotion; the "heel" of the foot contains the byssal gland. b. Foot probes into detrital material. c. Foot is retracted and adhering detritus is inserted between labial palps. GB = gill bar; L = labial palp; PD = particles of detritus.

carried in a dorsal ciliated tract of the mantle towards the labial palps. Some of this material is accepted by the palp surfaces and ingested, but the rest forms a loose clump in the region of the pedal gape. It may then be expelled by phasic adduction, or picked up by the foot and returned to the palps. The dorsal surface of the foot was seen on one occasion to return potential food that had been lost by the palps towards the mouth. Thus pedal-palp feeding continues to supplement the early suspension-feeding habit.

DISCUSSION

YONGE (1947) concludes that bivalve ctenidia cannot be effective filtration organs until they have reflexed and formed food grooves. ALLEN (1961) suggests that the action of the foot in juvenile *Pandora inaequalis* in creating an anterior feeding current might be found in other juveniles, since there would otherwise be no feeding mechanism between metamorphosis and ctenidial maturation. This is borne out by various reports cited in the Introduction above; in particular, KING (1986) demonstrates that in early *Pandora* juveniles "pedal-palp" feeding bridges that nutritional gap. There are several variations of this habit:



(1) **Locomotory pedal feeding:** the foot comes into contact with deposit material; pedal cilia collect particles and pass them to the labial palps or oral region.

(2) **Pedal probe-feeding:** the animal is stationary and the propodium probes for deposit material that adheres to mucus. Reflection of the foot brings the food into contact with the oral region.

(3) **Pedal sweep-feeding:** the stereotyped posteroanterior pedal feeding cycle. In most cases relatively large labial palps compact a rotating food bolus that is periodically ingested. The palps have no sorting function other than rejection of large, dense particles by centrifugation.

(4) **Interstitial pedal feeding:** the foot is thrust into a cavity that it has created in the substrate. Pedal cilia draw resuspended deposit material towards the mouth and labial palps, both on the surface of the foot and in an adoral current. We prefer this term to "interstitial suspension feeding" (LOPEZ & HOLOPAINEN, 1987).

In *Corbicula fluminea*, variations of locomotory pedal feeding and pedal probe-feeding occur when the organism is lying on a hard surface with a thin deposit film, when it is partially buried in sediment, and probably while moving through sediment. Pedal sweep-feeding is absent. There is interstitial pedal feeding, the cilia of both sides of the foot being involved when the organ is protracted into the substrate. The distinction between deposit feeding and suspension feeding in such cases becomes blurred. The extensive wandering of *Corbicula* specimens held in mud in aquaria indicates that locomotory pedal feeding permits this bivalve to continuously work and recycle the organically rich surface layers of sediment. WAY *et al.* (1990), in a report on the dynamics of filter feeding in *Corbicula*, comment on a pedal ciliary tract that may be capable of detritus feeding, and they conclude that the presence of food particles larger than 20 μm in the stomachs of their specimens may be due to other feeding methods than those involving gill filtration of suspended particles. The large amount of detritus that is routinely found in freshly collected field specimens is strong, if circumstantial, evidence of the importance of pedal feeding. *Corbicula* has excited curiosity concerning its ability to grow rapidly under conditions that do not appear to have the energetic resources to sustain such growth. Its success has been attributed to its speed of locomotion, adaptability, and the accommodating character of its pallial functional morphology (KRAEMER, 1977). These features, along with pedal feeding, allow the bivalve to maximize the uptake of particulate matter even when suspended food material is virtually absent.

In isolation, the case of pedal feeding in *Corbicula* may seem as exceptional as that of *Fimbria*. However, it is likely that a number of other mature bivalves, usually minute types, pedomorphically retain a combination of pedal feeding and anterior inhalant currents. The retention of a proportionately large foot could be pedomorphic. POPHAM (1940) notes that the proportionately large labial palps of *Mysella* indicate a significant role in direct particle collection as well as sorting. OCKELMANN & MUUS (1978) are of the opinion that feeding in *Mysella bidentata* is affected by the ciliary resuspension of sediment particles by the immobile extended foot, in the manner proposed by LOPEZ & HOLOPAINEN (1987) for *Pisidium*. But the pedal sweep-feeding of *Mysella* described above is a consistent habit that is similar to the mechanism found in juveniles of *Panope* and *Tridacna*. The behavior of juvenile *Abra alba* may also conform to such a pattern (AABEL, 1983). The juvenile pedal induction of an anterior inhalant, feeding current is preserved pedomorphically in minute bivalves such as *Lasaea rubra* (Galeommatacea) and *Turtonia minuta* (Veneracea) (OLDFIELD, 1955). Current research by the first author and K. Bartlett reveals pedal feeding in the small carditid species *Miodontiscus prolongatus*, and in the minute mytilid *Modiolaria taylori* (= *Musculus pygmaeus*). (We follow the opinion of Coan, personal communication, on these taxonomic revisions.) Moreover, juveniles of the venerid Manila clam *Tapes philippinarum* are probably exclusively pedal feeders until they attain the size of about 500 μm , an observation that has implications for nursery technology for this important commercial species (Reid, Bartlett & Lindsay, unpublished data).

The behavioral and neurophysiological capacity for various forms of pedal feeding exist in juvenile *Tridacna gigas*. Whether they are important in bridging the gap between metamorphosis and the establishment of ctenidial filtration, together with a functional symbiosis, remains to be determined. Peter Lee of James Cook University has undertaken a fuller study of the biology of early juveniles of this species. The nutritive significance of pedal feeding in giant clam juveniles is complicated by the existence of symbiotic zooxanthellae. The symbiosis is established in *Tridacna gigas* within 11 days of metamorphosis (HESLINGA *et al.*, 1984). Fitt (personal communication) surmises that the symbiosis may not contribute significantly to the economy of the early juvenile since much of the photosynthetic energy goes initially to the reproduction of the zooxanthellae. FITT *et al.* (1984) conclude that high mortality at the transition from pediveliger to juvenile is likely due to changes in the mode of acquiring food, and the nutri-

Figure 5

Photomicrographs of *Patinopecten* juveniles. a. Foot retracted, showing "heel" containing byssal gland. b. Foot probing while juvenile lies on side on hard surface. c. Foot probing fouled surface; four pairs of gill bars are present. d. Stomach contents of juvenile after pedally feeding on benthic diatom mat; arrows indicate diatoms. e. Foot retracted and appressed to labial palps. f. Juveniles byssally attached to fouled kinram. F = foot; GB = gill bar; H = "heel" containing byssus gland; L = labial palp.

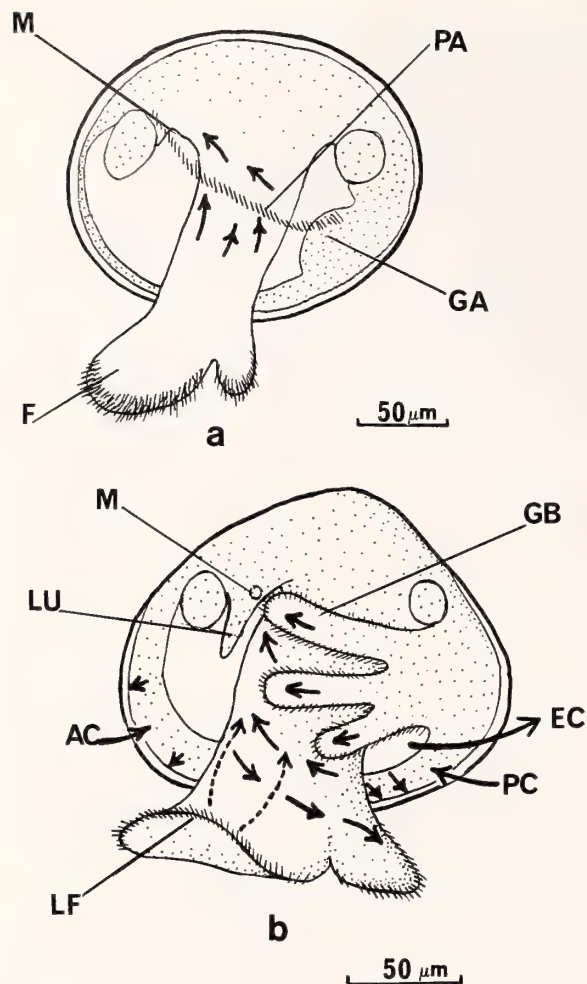


Figure 6.

Drawings of generalized *Nucula* juveniles (after MORTIMER, 1962). a. Pre-ctenidial stage. b. Proto-palpal stage. AC = anterior inhalant current; EC = exhalant current; F = foot; GA = gill anlage; GB = gill bar; LF = lateral flange of foot; LU = upper labial palp; M = position of mouth; PA = pallial arc; PC = posterior inhalant current.

tional requirement at this stage would not be likely to differ from the non-symbiotic clams.

The case of *Patinopekten yessoensis* is a caution against over-generalization since pedal sweep-feeding does not exist, and the early juveniles collect some suspended particles even before an efficient ctenidial morphology is in place (Ó FOIGHIL *et al.*, 1990). The juveniles usually employ pedal probe-feeding, and the foot also creates an anterior inhalant current. Similar behavior has been observed in early juveniles of the purple-hinged rock scallop *Crassadoma gigantea* (H. Miller, University of Victoria, personal communication). The absence of pedal sweep-feeding from this scallop juvenile may be correlated with the requirement of byssal attachment to a stable substrate for epifaunal inhabitants of turbulent water. *Panope abrupta* at-

taches to several large substrate components by byssus threads, but these are long enough (up to 10 cm) not to impede extensive working of the substrate over a relatively wide area by pedal feeding (KING, 1986). The persistence in the scallop and giant clam of a portion of the spectrum of pedal feeding found in burrowing clams supports the hypothesis that pedal feeding is a primitive component of bivalve functional morphology (KING, 1986). Therefore the feeding behavior of *Nucula*, which YONGE (1939, 1959) proposes as a model for the primitive bivalve, is of special interest.

MORTIMER (1962) studied *Nucula sulcata*, *N. tenuis*, and *N. turgida*. These all acquire pedal feeding ciliary tracts at metamorphosis, before the labial palps and ctenidia have developed. The foot ciliation is supplemented by a pair of "pallial arcs," narrow, ciliated pathways that pass from the gill rudiments across the dorsal mantle region towards the pedal acceptance tracts (Figure 6a). These species also demonstrate pedal sweep-feeding, described as an intermittent, back and forth motion, followed by foot retraction, that the author emphasizes as distinct from locomotion. The rudimentary palps provide a ciliary catchment area that directs pedally collected food to the mouth. As soon as the inner gill bars form, they make direct contact with the acceptance tracts of the foot, and particles filtered by them from the mantle water are carried by adoral ctenidial cilia on to the foot. At this stage, until the mature labial palp apparatus is developed, the ctenidia are the most important food-collecting organs. The strongest inhalant current during this period is posterior. Thus, *Nucula* proves the rule that the inhalant and exhalant currents in minute bivalves must be separated into anterior and posterior regions: in the intermediate stages of juvenile development the ctenidia are more important than the palps for feeding, and they create a posterior inhalant current while the mantle margins establish a posterior exhalant current (MORTIMER, 1962). Therefore, even in very small organisms, posterior inhalant and exhalant currents can co-exist. Parsimoniously, the position of the inhalant current should be considered to be an effect of the position and functional morphology of the major feeding organs.

Early postmetamorphic pedal feeding is the only thing that *Nucula* has in common with the other bivalves considered in this study. *Nucula* juveniles begin their pedal feeding before the labial palps are formed. Therefore, large labial palps are not an essential concomitant of pedal feeding. Moreover, the ctenidia bridge part of the gap between metamorphosis and the development of the complex food collecting apparatus of the mature form. STASEK (1961), MORTIMER (1962), and REID & BRAND (1986) agree that the prominent labial palp lamellae of protobranchs arose as primitive suspension feeding organs, and the elongation of the terminal pair of lamellar ridges as the detritus-collecting palp proboscides was a later specialization of the Nuculacea. The gills of mature Nuculidae, as STASEK (1961) notes, retain some particle-collecting role. Thus

nuculids, apart from their early pedal feeding, are exceptional in both the juvenile and mature forms. The early *Nucula* juvenile, rather than the adult, could be considered as a model for the primitive minute bivalve. From it, one evolutionary line opted for elaboration of the labial palps for food collection, with a proboscoidal deposit feeding habit as the final specialization. The other divergent line opted for specialization of the ctenidia as suspension-filtration organs. In any case pedal feeding remains the only consistent common feature.

YONGE (1959) is of the opinion that the molluscan ancestor of the bivalves locomoted with the foot and used small, undifferentiated labial palps to collect and sort detritus. The addition of a ciliary pedal feeding function produces the condition found in many of the juvenile and small bivalves that we describe above and that ALLEN (1985) similarly proposes as a primitive bivalve feeding mode.

What further light might the examination of pedal feeding shed on the original habit and habitat of bivalves: were they infaunal or epifaunal? Contrary to conventional wisdom the bivalve form is not a necessary correlation of movement through soft substrates. Many bivalves are epifaunal and other bivalved invertebrates such as brachiopods, ostracod crustaceans, and gastropod julids are epifaunal or planktonic. Most of the range of pedal feeding behaviors functions effectively at the surface of the substrate, whether it be particulate or solid. Therefore, primitive bivalves may have been epifaunal (STASEK, 1961; ALLEN, 1985; REID & BRAND, 1986), and the infaunal nature of many Recent mature bivalves may be irrelevant to the discussion of the origins of the class.

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Remarks on *Distorsio constricta*
(Broderip, 1833) and Related Species in the
Eastern Pacific Ocean, with the
Description of a New Species
(Gastropoda: Personidae)

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Abstract. The eastern Pacific species of the tonnacian genus *Distorsio* are reviewed; four species are recognized. Until recently, only two species of *Distorsio* were believed present in the eastern Pacific, namely *D. decussata* (Valenciennes, 1832) and *D. constricta* (Broderip, 1833). PARTH (1989a, b, 1991a), however, divided the long-held concept of *D. constricta* (*sensu stricto*) into three species. In addition to the nominate species, he recognized a second form as a new species, namely *D. minoruohnishii* Parth (1989b); and he referred a third form to *D. ridens* (Reeve, 1844a), a taxon recently assigned to the synonymy of *D. clathrata* (Lamarck, 1816) from the western Atlantic (EMERSON & SAGE, 1990a, b). We reject the attribution of the third form to *D. ridens* and describe it as a new species. The four species here recognized are *D. decussata* (Valenciennes, 1832), *D. constricta* (Broderip, 1833), *D. minoruohnishii* Parth, 1989, and *D. jenniernestae* Emerson & Piech, new species. A neotype is selected for *D. decussata*.

INTRODUCTION

PARTH (1989a, b, 1991a) has recently commented on the taxonomic status of the eastern Pacific species of *Distorsio*. In addition to the two west American species previously recognized by KEEN (1971:508), *D. decussata* (Valenciennes, 1832) and *D. constricta* (Broderip, 1833), he concluded that the latter is a complex comprised of three distinct taxa. He recognized, in addition to the nominate form, two other forms. For one of these newly recognized forms, he proposed a new species, *D. minoruohnishii* Parth (1989b), and he (PARTH, 1991a) referred the third form to *D. ridens* (Reeve, 1844), which was recently placed in

the synonymy of *D. clathrata* (Lamarck, 1816) by EMERSON & SAGE (1990a, b). We take this opportunity to review the status of these taxa on the basis of specimens from collections newly available to us.

Abbreviations

The following abbreviations for institutions and expeditions are used in the text.

AHF—Allan Hancock Foundation Pacific Expeditions, University of Southern California (collection transferred to LACMNH; for station data, see FRASER, 1943).

- AMNH—American Museum of Natural History, New York.
- BM(NH)—The Natural History Museum, London [formerly The British Museum (Natural History)].
- CASIZ—California Academy of Sciences, Invertebrate Zoology, San Francisco, California.
- DMNH—Delaware Museum of Natural History, Wilmington, Delaware.
- DSIR, GG—DSIR Geology and Geophysics, Lower Hutt, New Zealand.
- LACMNH—Los Angeles County Museum of Natural History, Los Angeles, California.
- NMNH—National Museum of Natural History, U.S. National Museum collection (USNM), Smithsonian Institution, Washington, D.C.
- P-AMNH—Puritan-American Museum of Natural History Expedition to Western Mexico (for station data, see EMERSON, 1958).
- TCE—Templeton Crocker Expeditions, New York Zoological Society (collection deposited in the AMNH and CASIZ; for station data, see BEEBE, 1937, 1938).

Historical Review of the Eastern Pacific *Distorsio constricta* Complex

Before PARTH's (1989–1991) recent work, only two species of *Distorsio* were generally recognized in eastern Pacific waters, namely *D. decussata* (Valenciennes, 1832) and *D. constricta* (Broderip, 1833). Owing largely to the failure of Valenciennes to illustrate his taxon, there had been a long period prior to the acceptance of this duospecies concept in which these taxa were confused (*cf.* TRYON, 1880: 35; DALL, 1908:319; PILSBRY, 1922:359; WOODRING, 1928: 101). These authors either did not recognize *D. decussata* as a west American species, or, if they did, they mistakenly considered *D. constricta* to be a junior synonym of *D. decussata*. Eventually, PILSBRY & OLSSON (1941:40, pl. 5, figs. 9, 12) clarified the differences between the two taxa by stating: "It has been commonly believed that but one *Distorsio* was found living in the Panama Province but actually there are 2 well-marked species, *Distorsio decussatus* Val., described from Acapulco, and *Distorsio constrictus* Broderip, described from Santa Elena, and well figured by Reeve, (1844, Conch. Icon., *Triton*, pl. 12, fig. 41). The 2 species are easily separated even when they occur together, as they do at several places along the Ecuadorian and Panamic coast. *Distorsio constrictus* is a strongly distorted shell, the aperture and particularly the inner lip being strongly tuberculate with a short but strongly recurved anterior canal. *Distorsio decussatus* is a more slender, regular and thinner shell; the parietal callus is smoother, and the anterior canal is longer and nearly straight. In both species the spiral cord on the shoulder or periphery of the body-whorl is doubled." The erroneous monospecies concept, however, was still held by some workers as late as KILIAS' review (1973:207, 208) of the "Cymatiidae."

Actually Dr. Woodring had accepted the duo status (*in litt.*, to W. K. Emerson, 1 May 1954) following the publication of a catalog of the genus *Distorsio* (EMERSON & PUFFER, 1953:98, 99; see WOODRING, 1959:205) and this concept was held by virtually all workers (*cf.* LEWIS, 1972: 46). Therefore, until recently, *D. constricta* and *D. decussata* were believed to be largely sympatric, the former known from the Gulf of California, Mexico, to Mancora, Ecuador, and the latter from the Gulf of California to Manta, Ecuador (KEEN, 1971:508).

PARTH (1989a:53, illus. 2nd row, right side) reported two "typical" specimens of the western Pacific species *Distorsio habei* LEWIS (1972:38, figs. 38, 39) in a lot from "Oaxaca," Mexico, mixed with specimens of *D. decussata* (VALENCIENNES, 1832:306) and *D. constricta* (BRODERIP, 1833:5). According to Dr. Beu (*in litt.*, to W. K. Emerson, 25 October 1991), a specimen sent to him by M. Parth as *D. habei*, from "Oaxaca," Mexico, is a specimen of *D. perdistorta* FULTON (1938:55, pl. 3, fig. 3, 3a), again a species not otherwise known from the eastern Pacific. The validity of this record was previously questioned (EMERSON, 1991:68, footnote 30). Until eastern Pacific specimens of *D. habei* with unequivocal locality data are forthcoming, we question Parth's west American records for this taxon. In the same paper, PARTH (1989a:52, illus. 2nd row, right side) figured a specimen from "Oaxaca" as "*D. constricta constricta*." This is the same specimen he subsequently designated as paratype 8 of his new species, *Distorsio (Distorsio) minoruohnishii* Parth (1989b), which he shortly thereafter differentiated from *D. constricta*.

Subsequently, PARTH (1991a) called attention to the presence of a third morphological form in the *Distorsio constricta* complex. He believed that it was referable to *D. ridens* (Reeve, 1844a), which was recently referred to the synonymy of *D. clathrata* (Lamarck, 1816), a western Atlantic species (EMERSON & SAGE, 1990a, b). Thus, he split this complex into three taxa, namely *D. constricta* (Broderip, 1833), *D. minoruohnishii* Parth, 1989, and *D. ridens* (Reeve, 1844), *sensu* PARTH (1991a).

Before discussing the status of *Distorsio ridens* and our reasons for rejecting Parth's assignment of the third form of this complex to *D. ridens*, we should comment on this newly recognized form and its relation to *D. constricta* (*sensu stricto*) and *D. minoruohnishii*. Fortunately, three syntypes of *D. constricta* are extant in The Natural History Museum, London (BM[NH] 1989016; Figures 2, 3), and there is no doubt of the concept of this taxon. Both *D. constricta* and the third form believed to be *D. ridens* by Parth have larger, more distorted shells than *D. minoruohnishii*, of which the largest known specimen is 51.6 mm in height (AMNH 232209); in contrast, the height of *D. constricta* and the third form may exceed 60 mm (64.3 mm [LACMNH 70-15.12] and 64.1 mm [AMNH 232215], respectively).

PARTH (1991a:10) noted two major differences between *Distorsio constricta* and the form he believed referable to

D. ridens, namely the presence of a "big notch" on the "upper part of the outer lip, almost at the second tooth level"; and, secondly, the "color of the inner and outer lip, subdiscoidal-shaped, ranges from light orange to dark brown." He did not mention the large white area of the parietal shield that extends into aperture. As noted by Parth, the third form has a distinctive groove on the interior of the outer lip located at the periphery of the body whorl. This "big notch" (Figure 18), however, is not formed in juvenile specimens, for example those with fewer than six postnuclear whorls (Figures 16–18). This groove is a prominent feature in mature specimens and is lacking at all growth stages in *D. constricta* and *D. minoruohnishii*. Also, the color pattern and sculptural details differ markedly between *D. constricta* and the third species, as noted by Parth. We do agree that there are three distinct forms in this complex, but we disagree with Parth's belief that the third form is referable to *D. ridens*.

Distorsio ridens (Reeve, 1844a, b) was for a long time an enigmatic species, the status of which has been reviewed in recent years by LEWIS (1972), EMERSON & SAGE (1990a, b), and, most recently, by PARTH (1991a). LEWIS (1972) could not locate the figured specimen in The Natural History Museum, London, and he selected a lectotype in the American Museum of Natural History (AMNH 6369). He believed *D. ridens* represented a valid taxon of probable Indo-Pacific origin of which additional specimens had yet to be discovered. EMERSON & SAGE (1990a, b) concluded that Reeve's taxon was referable to *D. clathrata*, a common western Atlantic inhabitant. PARTH (1991a) considered the third form in this eastern Pacific complex to be the taxon that REEVE (1844a:fig. 46) described and illustrated as "*Triton*" *ridens* from the "Philippine Islands." We reject this attribution.

We describe herein this third form as a new species and reject its allocation to *Distorsio ridens* for the following reasons:

(1) The degree of distortion depicted in REEVE's illustration (1844a:fig. 46) of *D. ridens* is slight, whereas in the new species, as well as in the illustration by REEVE (1844a:fig. 41) of *D. constricta*, the specimens are severely distorted (cf. Figures 1 and 9 with Figures 5–8). Furthermore, all of the specimens of the new species we have examined, some 40 specimens, as well as the specimens figured by PARTH (1990a:11, 1st row) have similar degrees of distortion. We believe that the artist, G. B. Sowerby, II, certainly would have recognized the distorted nature of the shell, as he did for *D. constricta*, if he had had before him a specimen of the new species to draw. In contrast, Reeve's figure of *D. ridens* depicts a shell with a degree of distortion that is similar to that of Lewis' lectotype of *D. ridens* and to specimens of *D. clathrata* from the western Atlantic Ocean (cf. Figure 9 with Figure 12).

(2) The sculptural details of the parietal shield in the drawing of *D. ridens* (Figure 9) show the axial ribs extending from the suture to the base of the parietal shield.

In mature specimens of the new species, the axial ribs are posteriorly wanting, as they extend only about half the distance from the suture to the middle portion of the shield (Figures 6, 8). The axial ribs, however, do extend from the suture to the aperture in *D. clathrata* (cf. Figure 9 with Figures 10, 12). The early plicae on the mid to lower columellar wall are prominent and the first plica is bifid in REEVE's (1844a) drawing of *D. ridens*, but they are small and not bifid in the new species. Moreover, they are large and not uncommonly bifid in *D. clathrata* (see EMERSON & SAGE, 1990a:figs. 1, 14, 15).

(3) There is no mention in REEVE's (1844a, b) descriptions of *D. ridens* of a depression ("big notch") on the outer lip, nor is one depicted in the REEVE's illustration (1844a:fig. 46). The wrinkle-like fold above the first anteriorly placed plica on the outer lip as shown in Reeve's drawing (Figure 9 herein) is not uncommonly found on the outer lip of *D. clathrata* and is situated above the location of the "big notch" of the new species (cf. Figures 9, 10, 12).

(4) The drawing of *D. ridens* (REEVE, 1844a:fig. 46; Figure 9 herein) shows the orange-brown pigmentation extending over the surface of the parietal shield as is often the case in specimens of *D. clathrata* (Figure 12). In the new species, the columellar surface immediately above the aperture is a glossy white (Figures 6, 8).

PARTH (1991a:10) objected to the placement of *Distorsio ridens* in the synonymy of *D. clathrata* largely on the basis of two criteria that do not characterize *D. clathrata*. These are the single cording of the ribs on the dorsum and the length of the siphonal canal. In the new species, the spiral cords at the periphery of the whorls are "duplicated," or are even "triplicated" in some specimens. REEVE's (1844a:sp. 46) description of *D. ridens* states that the "whorls [are] elegantly latticed with prominent, narrow, raised ridges, transverse ridges duplicate." Actually, the apertural view of REEVE's illustration (1844a:fig. 46; Figure 9 herein) does not project the presence of "duplicated" spiral cords on the periphery of the body whorl. Unfortunately, a view of the dorsal surface of the illustrated specimen was not provided by Reeve. The presence of a double cord would be, of course, in contrast to the single spiral cord on the periphery of *D. clathrata* (Figures 11, 12). The duplicate sculpture is characteristic of *D. decussata* as noted by EMERSON & SAGE (1990a:134), and *D. ridens* was referred to this taxon by BEU (1985:62) and PARTH (1989a:54). Beu (*in litt.*, to W. K. Emerson, 17 January 1990) subsequently concluded that *D. ridens* was referable to *D. clathrata* based on the identify of the lectotype of *D. ridens* (Figures 10, 11).

PARTH (1991a:10) also believed that Reeve had never personally examined specimens of *Distorsio clathrata* before he described *D. ridens*, and, therefore, the specimen illustrated by REEVE (1844:fig. 46) could not have been referable to *D. clathrata*. It should be noted, however, that Reeve was an associate of Broderip and had access to his collection. BRODERIP (1833:5) in his description of *D. constricta*

Table 1
Shell comparisons of the four Recent species of eastern Pacific *Distorsio*.

	<i>Distorsio constricta</i>	<i>Distorsio minoruohnishii</i>	<i>Distorsio jenniernestae</i>	<i>Distorsio decussata</i>
Distortion	Most distorted.	Slightly less than <i>D. constricta</i> .	Almost the same as <i>D. constricta</i> .	Least distorted.
Sculpture of body whorl	8–13 major axial ribs forming nodules where they cross spiral cords, double at the periphery.	9–11 major axial ribs forming nodules where they cross spiral cords. 12–14 major spiral cords, double at the periphery.	10–13 major axial ribs forming nodules where they cross spiral cords, double or triple at the periphery.	12–17 major axial ribs forming nodules where they cross spiral cords. 13 major spiral cords, single or double at the periphery.
Color	Body tan, darkest of the 4 species. Shield and outer lip darker than the body. Aperture white.	Body tan to straw color, early whorls darker. Dark band around the periphery of body whorl. Shield and outer lip cream color. Aperture white.	Body varying between straw and white. Shield and outer lip have dark brown edge. Aperture white.	Body mostly white, some straw color. Shield and lip white with some light tan staining around the edge. Aperture white.
Parietal shield	Strong beading. Lower left-hand edge of shield just barely away from the body.	Weak beading. Left-hand edge of shield noticeably extends away from the body.	Smooth to low beading. Left-hand edge of shield noticeably extends away from the body.	Smooth to low beading. Left-hand edge of shield noticeably extends away from the body.
Siphonal canal	Open, angles slightly to the right, recurves to the back. Shortest canal of the 4 species.	Open, angles slightly to the right, recurves to the back. Slightly longer than <i>D. jenniernestae</i> .	Open, angles slightly to the right, recurves to the back. Slightly longer than <i>D. constricta</i> .	Open, straight, recurves to the back. Longest canal of the 4 species.
Outer edge of lip	Thick, straight.	Thinner than <i>D. constricta</i> flaring at the lower edge.	Thinner than <i>D. minoruohnishii</i> . Flaring at the lower edge. Lip with a marked depression at the periphery of the body whorl, unique to this species.	Thin like <i>D. jenniernestae</i> and flaring at the lower edge.
Inner edge of lip	8 plicae, 3rd one slightly larger.	8 plicae, 3rd one slightly larger.	8 plicae, very prominent 3rd plica.	5–8 plicae, very prominent 3rd plica.
Prominent columellar plicae	1 in posterior end. 1 on left side above siphonal canal extending into aperture.	1 in posterior end. 1–2 on left side above siphonal canal extending into aperture.	1 in posterior end. 1 on left side above siphonal canal extending into the aperture.	1 in posterior end. No plicae extending into the aperture above the siphonal canal.
Periostracum (outer surface)	Tan-brown color with very numerous soft, short hairs forming a velvet texture.	Tan-brown color with very numerous soft, short hairs forming a velvet texture. Longer individual hairs at many of the intersections of the axial ribs and spiral cords.	Tan-brown color with very numerous soft, short hairs forming a velvet texture. Longer darker hairs forming clusters along the axial ribs.	Dark-dark brown colored (covering a thin straw colored basal layer) with longer, individual hairs at the intersection of the axial ribs and spiral cords.

actually compared it with *D. clathrata*. Furthermore, REEVE (1844a:sp. 45) cited "*Triton clathratus* Lamarck" [= *Distorsio clathrata*] in the synonymy of "*Triton cancellinus*" [= *D. reticularis* Linné, *vide* BEU, 1987:314], and he subsequently compared *D. ridens* with "*Triton cancellinus*" (REEVE, 1844b:115). The status of *D. clathrata* at that time was poorly understood and specimens of *D. clathrata* were confused with specimens of *D. reticularis* from the Indo-Pacific (PUFFER, 1953:109).

The siphonal canal, Parth's second point of difference, is indeed longer and less recurved in *Distorsio clathrata* than in the new species. However, the siphonal canal is shortened by breakage in the lectotype of *D. ridens* (Figure 10) and this may have been the case of the specimen figured by REEVE (1844a:fig. 46), which is depicted with a narrow siphonal canal, unlike the widely open canal of the new species (*cf.* Figure 9 with Figures 6, 8).

Despite these possible disparities, the gross angular dis-

tortion of the whorls that characterizes the new species, together with the other differences (Table 1), serves in our opinion to separate it from *Distorsio ridens*.

We take pleasure in naming the new species for Jennifer Ernest, the daughter of Gladys and James Ernest, who kindly provided us with critical specimens for this review.

SYSTEMATIC TREATMENT

Superfamily TONNACEA Suter, 1913

Family PERSONIDAE Gray, 1854

Genus *Distorsio* Röding, 1798

Synonyms: *Distortrix* Link, 1807; *Persona* Montfort, 1810; *Distorta* Perry, 1811; and *Rhysema* Clench & Turner, 1957; see BEU (1987:310; 1988:89).

Type species: *Distorsio anus* (Linné, 1758) by subsequent designation of PILSBRY (1922:357).

Distorsio (Distorsio) constricta (Broderip, 1833)

(Figures 1–4, 23)

Triton constrictus BRODERIP, 1833:5; REEVE, 1844: *Triton* sp. 41, pl. 12, fig. 41 [May, 1844].

Distorsio constrictus Brod. [erip]: TRYON, 1880:35, in part, pl. 17, fig. 176 only [copy of REEVE, 1844:fig. 41], not *Distorsio cancellinus* Roissy, *sensu* TYRON, 1880:35; PILSBRY & OLSSON, 1941:40, pl. 5, fig. 12, Manta, Ecuador (Recent specimen); KILIAS, 1973:203, 204, fig. 145, "Peru," in part, excluding references to *Distorsio decussata* (Valenciennes, 1832).

Type locality: "Hab. ad Montem Christi et Xipixapi" (BRODERIP, 1833:5). "Monte Christi and Xipixapi, West Columbia (dredged from sandy mud at a depth of from seven to ten fathoms; Cumings)" (REEVE, 1844). Restricted by M. SMITH (1944:23) to St. Elena [= Xipixapa], Ecuador.

Type depository: Lectotype, 60.8 × 36.1 mm (Figures 2, 3) and 2 paralectotypes, 60.7 × 34.6 and 54.7 × 31.1 mm, respectively (BM[NH] 198016).

Distribution: Islas Murcielago, Guanacaste Prov., Costa Rica, to Manta, Ecuador.

Specimens examined: COSTA RICA: Off Quepos, Puntarenas Prov. (9°22.20'N, 84°09.3'W) in 23 m, 1 specimen, J. McLean *leg.* (LACMNH 72-59.1); Isla San Pedrito, Islas Murcielago (10°51.5'N, 86°57.95'W), in 2.4–4 m, 1 specimen, J. McLean *leg.* (LACMNH 72-22.2). PANAMA: Golfo de Panamá, Isla Venado, –2.4 tide, 5 April 1981, 1 specimen (AMNH 207600), *ex* H. DuShane coll.; Isla Venado, 2 specimens (LACMNH 34643); Isla Venado, –1.8 tide, in silty runnels, night 16 March 1980, 2 specimens (AMNH 232205), *ex* H. DuShane coll.; Isla Venado, beach, 2 specimens (AMNH 232206), *ex* A. Marti coll.; Isla Venado, 8 March 1970, 1 specimen, J. McLean *leg.* (LACMNH 70-15.12); Isla Bono, Islas Otoque, in 9–

27 m, 2 specimens, J. McLean *leg.* (LACMNH 65-21.9); Isla Secas, Chiriqui Prov., in 27 m, AHF station 34-125, 1 specimen (LACMNH 34-125.4); Bahía Honda, Veraguas Prov., in 9–15 m, AHF station 33-120, 1 specimen (LACMNH 33-120.2); "Panama Bay," intertidally, in sandy mud, 4 specimens (AMNH 232191), *ex* Abbey Specimen Shells. COLOMBIA: Off Isla Gorgona, in 18 m, AHF station 34-98, 1 specimen (LACMNH 34-98.2). ECUADOR: Off Cape San Francisco, in 27 m, AHF station 38-118, 1 specimen (LACMNH 38-118.6); Manta, J. Marks *leg.* (CASIZ 37339).

Remarks: There are in The Natural History Museum, London, three specimens (BM[NH] 198016) that were identified as syntypes by Aileen Blake (A. Beu, *in litt.*, to W. K. Emerson, 25 October 1991). These are large specimens (H = 61.2, 60.9, and 54.7 mm), each of which is badly faded, but otherwise well preserved. The second largest, which has some of the periostracum still preserved, appears to be the specimen illustrated by REEVE (1844a: fig. 41) and is here selected as the lectotype (*cf.* Figure 1 with Figures 2, 3). The old labels accompanying the syntypes cite "Monte Christi and Xipixapi" as the type localities, which are BRODERIP's (1833:5) citations for the habitat.

Distorsio (Distorsio) minoruohnishii

Parth, 1989

(Figures 13–15a, b, 25)

Distorsio constricta constricta (Broderip): PARTH, 1989a:52, in part, 6 unnumbered figs., specimen in 3rd row, on right side, "Oaxaca, W. messico" [sic]; not *Distorsio constricta* (Broderip, 1833).

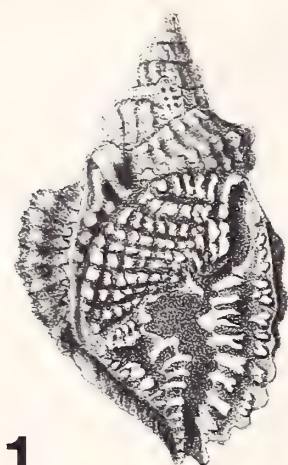
Distorsio minoruohnishii PARTH, 1989b:8–11, holotype illustrated on p. 8, holotype and 9 paratypes illustrated on p. 11; PARTH, 1991a:11, 3rd row, first two specimens illustrated on left side of plate.

Type depositories: Holotype (BM[NH] 1990025), *fide* PARTH (1991b:21; here illustrated in Figure 15a, b). Nine paratypes cited and illustrated (PARTH, 1991a:9) from Mexico and Panama. One of these, paratype 2, from the "Bay of Chiriqui, Panama" is deposited in the AMNH (246024).

Type locality: "Oaxaca, Mexico" [the Mexican state] cited for the holotype (PARTH, 1989b:9). Here restricted to off "Isla Macapule, [Sinaloa], Mexico" (PARTH, 1989b:9; paratype 9; and 28 topotypes AMNH 174247, 186686, and 232198; Figures 13, 14).

Distribution: Golfo de California, Mexico, to off Tumbes, Peru.

Specimens examined: MEXICO: Gulf of California, Baja California Norte: Off Isla San José, P-AMNH Station 116, in 67 to 73 m, 2 specimens (AMNH 76180); off Puerto Escondido, P-AMNH Station 138, in 33 to 36 m, 1 specimen (AMNH 76493); Baja California Sur, Punta



1



2



3



4



5



6



7



8



9



10



11



12

Arena Bank, TCE Station 136-D-17, in 82 m, 4 specimens (AMNH 94097); Gorda Bank, TCE Station 150-D-32, in 165 m, 29 specimens (AMNH 140269). Bahía Los Frailes, P-AMNH Station 89, in 36 to 73 m, 2 specimens (AMNH 75807); off Punta Coyote, La Paz Bay, dredged in 45 m, 3 specimens, *ex* Abbey Specimen Shells (AMNH 183767); south of La Paz, dredged, 5 specimens, *ex* C. Skoglund coll. (AMNH 186684). Sonora: Bahía Kino, trawled, 2 specimens, A. Luna *leg.* (AMNH 232210); off Guaymas, shrimp boat, 2 specimens, *ex* T. Rice coll. (AMNH 180703); Puerto Guaymas, in 33 m, 4 specimens, *ex* R. Purdy coll. (AMNH 240421); off Guaymas, dredged by fishermen, 1 specimen, G. Eddison coll. (AMNH 232203). Sinaloa, Isla Macapule (south of Bahía de Topolobampo), in 45 m, 22 specimens (together with 4 specimens of *Distorsio jenniernestae*, sp. nov.), A. Luna *leg.*, *ex* H. DuShane coll. (AMNH 174247, 232198); same locality and data, *ex* C. Skoglund coll., 6 specimens (AMNH 186686). Nayarit, Islas Las Tres Marías, off Isla María Magdalena, P-AMNH Station 71, in 23 to 27 m, 1 specimen (AMNH 75379), Isla María Madre, P-AMNH Station 72, in 25 to 27 m, 1 specimen (AMNH 75529); Colima, off Manzanillo, in 15–22 m, 4 specimens, *ex* S. Bennett coll. (AMNH 232207); off Manzanillo, in 31 m, 2 specimens, *ex* H. DuShane coll. (AMNH 232204). COSTA RICA: Isla Tortuga, 1 specimen, *ex* K. Vaught coll. (AMNH 214705); Bahía Ballenas, in 64–73 m, TCE Station 213-D-11-17, in 64 m, 3 specimens (AMNH 85336a) (together with 2 specimens of *D. jenniernestae*); between Bahía Elena and Bahía Juanillo (85°46.13'W), in 26–53 m, 2 specimens (LACMNH 72-12.4); off Bahía Herradura (9°38.8'N, 84°40.8'W), in 37 m, 3 specimens, J. McLean *leg.* (LACMNH 72-54.4). PANAMA: Golfo de Panamá, Palo Seco, 3 specimens, E. Bergeron *leg.* (AMNH 156620); Isla de los Perlas, 3 specimens (AMNH 123002); Golfo de Montijo, off Isla Gobernadora, 1 specimen, *ex* B. Piech coll. (AMNH 239212). Golfo de Chiriquí, paratype 2, *ex* M. Parth coll. (AMNH 246024). COLOMBIA: Off Puerto Utria, in 82 m, AHF Station 35-54, 1 specimen (LACMNH 35-54.1). ECUADOR: Off Santa Elena, in 15–18 m, AHF Station 34-83, 1 specimen (LACMNH 34-83.6). PERU: Between Caleta La Cruz and Puerto Pizzaro, off Tumbes (3°28'S, 80°36'W), in 9–33 m, 3 specimens,

J. McLean *leg.* (LACMNH 72-83.6). (An additional 40+ lots in the LACMNH and AMNH collections from Mexico, Costa Rica, and Panama were examined but are not recorded owing to redundancy.)

Remarks: The holotype (BM[NH] 1990025; Figure 15a, b herein) is a small, well-preserved, crabbed specimen, with 6 postnuclear whorls, and measures 38.3 mm in height and 21.3 mm in width. Mature examples with 7 postnuclear whorls attain 51+ mm in height (AMNH 232209, Gulf of California). Some of the more ovate specimens approach Philippine specimens of *Distorsio habei* in many characters, but differ mostly in the degree of distortion of the whorls, in some of the details of the apertural dentition, and in the possession of a less recurved siphonal canal (*cf.* Figures 13–15 with Figures 19, 20).

Distorsio (Distorsio) jenniernestae

Emerson & Piech, sp. nov.

(Figures 5–8, 16–18, 24)

Distorsio (Rhysema) constricta (Broderip): EMERSON & OLD, 1963:26, in part, fig. 24, off Isla Tiburón, Gulf of California; KEEN, 1971:508, in part, fig. 962, Gorda Bank, Gulf of California (CASIZ coll.); LEWIS, 1972:45, in part, fig. 41, off Santa Cruz Id., Galapagos Islands; KERSTITCH, 1989:45, in part, fig. 89 (colored photograph of living animal); not *Distorsio constricta* (Broderip).

Description: Shell, large (attaining 60+ mm in height), fusiform, very much distorted, spire attenuately acuminate (spire produced at an angle of about 45°), with 7 postnuclear whorls angulated at the upper part, and 2½ smooth, glossy embryonic whorls (Figure 24). Surface of body whorl sculptured with 10 to 13 major axial ribs and numerous spiral cords forming nodules at the intersections; nodules on periphery of the shoulder largest, crossed by 2 or 3 spiral cords. Aperture large, outer lip thin at edge with 3 distinct plicae (the third being the largest) on the upper (posterior) portion, disjunct from the outer edge, and with 5 or 6 broken denticles on the lower (anterior) portion. Outer lip with a large depression (groove) formed

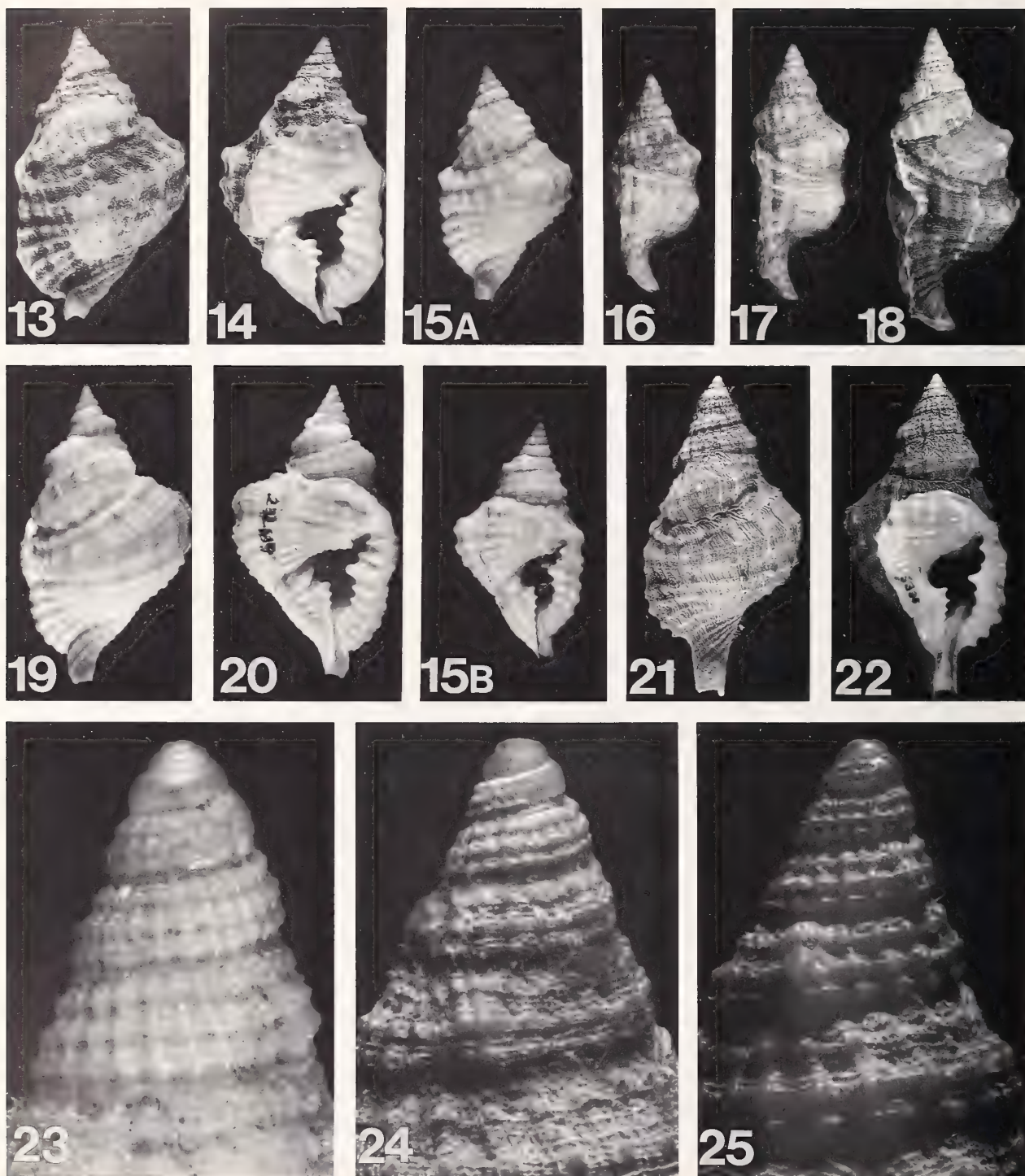
Explanation of Figures 1 to 12

Figures 1–4. *Distorsio constricta* (Reeve). Figure 1: copy of illustration of *Triton constrictus* Broderip (REEVE, 1844a: pl. 12, fig. 41). Figures 2, 3: lectotype of *Triton constrictus* (BM[NH] 198016). Figure 4: specimen with fully developed apertural morphology (LACMNH 70-15.12).

Figures 5–8. *Distorsio jenniernestae*, sp. nov. Figures 5, 6: holotype (AMNH 232214). Figures 7, 8: paratype (AMNH 232215).

Figures 9–12. *Distorsio clathrata* (Lamarck, 1816). Figure 9: copy of illustration of *Triton ridens* REEVE (1844a: pl. 12, fig. 46). Figures 10, 11: lectotype of *Distorsio ridens* (AMNH 6369). Figure 12: specimen from off Punta Patuca, Atlantic Honduras (AMNH 238556).

Figures 1–12, ×1.



Explanation of Figures 13 to 25

Figures 13–15a, b. *Distorsio minoruohnishii* Parth, 1989. Figures 13, 14: specimen with fully developed apertural morphology, off Isla Macapule, Sinaloa, Mexico, topotype (AMNH 232198). Figures 15a, b: holotype (BM[NH] 1990025).

Figures 16–18. *Distorsio jenniernestae*, sp. nov., a growth series showing the prominent marginal groove developed in the largest specimen (Figure 18), off Isla Macapule, Sinaloa, Mexico (AMNH 232199).

at the periphery of the body whorl (not developed in specimens with fewer than 6 postnuclear whorls; see Figures 16–18). Parietal shield extending to the suture, thin with 4 to 6 axial ribs below the suture, replaced by 5 or more weak spiral ribs below, blending into the aperture. Columellar inner edge with 8–10 plicae, with the upper 2 (posterior) the largest. Siphonal canal broadly open, short, and recurved slightly upwards. Basic color white and straw-tan, early whorls darker tan, parietal shield and outer lip orange-brown with streaks of white, aperture glossy white. Animal orange-brown with white blotches (KERSTITCH, 1989:fig. 89). Periostracum tan-brown, thin, flaky, with numerous short hairs; darker hairs in clusters along the axial ribs. Operculum small, oblong, terminal with several concentric fine lines on outer surface, and with wide marginal, raised callus and broad bands of uneven rings on inner surface.

Type locality: Dredged in 73 m between Isla Cébaco and Isla Coiba, off the Pacific coast of Veraguas, Panama, J. Ernest, 1991.

Type depositories: Holotype (AMNH 232214; Figures 5, 6; H = 59.9 mm, W = 32.3 mm) and 4 paratypes (AMNH 232215; Figures 7, 8); 2 paratypes (USNM 860245); 2 paratypes (DMNH 189600); 1 paratype (DSIR-GG WM 15345) and 10 paratypes (B. J. Piech coll.); all from the type locality.

Distribution: Golfo de California, Mexico, to the Golfo de Panamá, and the Galapagos Islands.

Specimens examined: MEXICO: Golfo de California, off Isla Tiburón, P-AMNH Station 162, in 73 m (AMNH 77066), illustrated as *Distorsio constricta* (Broderip) by EMERSON & OLD (1963:27, fig. 24); off Isla Angel de la Guardia, in 93–102 m, AHF station 40-29, 1 specimen (LACMNH 40-29.1). Between Isla Partida and Espiritu Santo, in 73–165 m, AHF Station 60-61, 1 specimen (LACMNH 60-6.9); off Punta Coyote, Bahía de La Paz, Baja California Sur, dredged in 45 m, by commercial fishermen, 2 specimens (AMNH 232192) *ex* Abbey Specimen Shells. Off Cabo Pulmo, in 91 m, AHF 1732-49, 1 specimen (LACMNH 49-73.1); off Cabo San Lucas, Baja California Sur, in 137 m, AHF Station 618-37, 1 specimen (LACMNH 37-19.2); Bahía Guaymas, Sonora, dredged in 30 m by fishermen, 1 specimen (AMNH 240421a), *ex*

R. Purdy coll.; off Cabo Haro, Sonora, in 183 m, AHF station 60-31, 3 specimens (LACMNH 60-3.4). Isla Macapule, Sinaloa, dredged in 45 m by A. Luna, 4 specimens (AMNH 232199), *ex* S. Bennett coll. COSTA RICA: Off Bahía de Ballenas, Golfo de Nicoya, in 64 to 82 m, TCE Station 213-0-11-17, in 64 m, 2 specimens (AMNH 85336) (together with 2 specimens of *D. minoruohnishii* Parth); off Isla del Cano (8°45'N, 84°0'W) in 73–82 m, 1 specimen, J. McLean *leg.* (LACMNH 72-67.2). PANAMA: Golfo de Chiriquí, 1 specimen, *ex* M. Parth coll. (AMNH 232183); between Isla Cébaco and Isla Coiba, in 73 m, type locality, 20 specimens. ECUADOR: Galapagos Islands, SE. of Isla Daphne (0°27'S, 90°21.8'W), AHF Station 38-48, in 101 m, 1 specimen (LACMNH 38-48.1).

Remarks: Mature specimens of the new species may be distinguished without difficulty from the other three species of *Distorsio* recognized in the eastern Pacific Ocean (Table 1). The “big notch” on the outer lip is present in specimens with six or more postnuclear whorls (*cf.* Figures 16–18). The function, if any, of this groove is not known. Joseph Houbbrick (personal communication, 24 September 1991) speculated that perhaps it serves as an egg laying sinus or possibly a penile groove, owing to the location of the bursa copulatrix and penis, respectively, in the related families Ranellidae and Bursidae (HOUBRICK & FRETTER, 1969: 417). With the exception of *Distorsio decussata*, the embryonic whorls of all the west American species are similar, consisting of 2½ smooth, glossy whorls. This character is not useful in separating the other three taxa (Figures 23–25).

The new species is distributed intertidally to depths of 137 m from near the head of the Gulf of California to the Gulf of Panama. It is also known from the Galapagos Islands in 101 m. *Distorsio minoruohnishii* is largely sympatric in range with the new species in depths to 80+ m, but it also extends southward to northern Peru. In contrast, *D. constricta* is restricted in distribution to the southern part of the Panamic faunal province, with records from Costa Rica to Ecuador, in tidal waters to depths of 27 m.

The interspecific relationships of the new species and the three other west American species are somewhat difficult to interpret. *Distorsio constricta* in the Pacific and *D. macgintyi* EMERSON & PUFFER (1953:101; OLSSON & MCGINTY, 1951:27, pl. 1, figs. 5, 6, 9) in the Atlantic were considered to be geographical subspecies (BEU, 1985:

Figures 19, 20. *Distorsio habei* Lewis, 1972, off Panglao, Bohol, Philippines (AMNH 232189).

Figures 21, 22. *Distorsio decussata* (Valenciennes, 1832), neotype, off Punta Arena, Gulf of California, TCE Station 136-D-21, in 82 m (AMNH 85335).

Figures 23–25. Spires enlarged to show embryonic whorls. Figure 23: *D. constricta* (AMNH 232205). Figure 24: *D. jenniernestae*, sp. nov. (AMNH 232199, specimen shown in Figure 16). Figure 25: *D. minoruohnishii* (AMNH 174247).

Figures 13–22, ×1; Figures 23–25, ×3.5.

62; EMERSON, 1991:73, table 4) before the discovery of more than one species in the *D. constricta* complex. OLSSON & MCGINTY (1951:27), LEWIS (1972:46), and others believed that *D. simillima* (SOWERBY, 1850:48) from the Miocene of the Caribbean region was the precursor of this cognate pair. Unfortunately, Sowerby did not provide an illustration of his *D. simillima* from the Dominican Republic and this name has been applied to various species concepts (cf. WOODRING, 1959:206). PFLUG (1961:39–41, pl. 9, figs. 4, 6, 9) selected and illustrated a lectotype of *D. simillima*. On the basis of this lectotype designation, *D. simillima* is not referable to the *D. constricta* complex. Pflug's lectotype is clearly related to *D. decussata* (VALENCIENNES, 1832:306). The closeness of the lectotype in shell characters to the Mid-American Pliocene *D. gatunensis* TOULA (1909:700, pl. 25, fig. 10; BROWN & PILSBRY, 1911:356, fig. 8; WOODRING, 1959:205, pl. 34, figs. 7, 8; AGUILAR & FISCHER, 1986:223, pl. 2, figs. 13, 14) suggests that Toulou's taxon is closely related to *D. simillima*. MAURY (1917:107, pl. 17, figs. 4, 5) considered *D. gatunensis* a junior synonym of *D. simillima*. Beu (*in litt.*, to W. K. Emerson, 25 October 1991), however, believes *D. gatunensis* to be identical with *D. decussata*. This leaves the Pliocene precursor of the *D. constricta* complex (WOODRING, 1928:pl. 18, fig. 9 and pl. 19, fig. 1) from Panama and elsewhere in the New World tropics without a name. Further study is needed to determine if the fossil populations of *D. constricta* require specific recognition. *Distorsio crassidens* (CONRAD, 1848:118, pl. 11, fig. 40; MACNEIL & DOCKERY, 184:121, pl. 31, figs. 5, 6) from the Vicksburg Group of Mississippi (Oligocene) and *D. simillima* (Mio-Pliocene) appear to be linear antecedents of *D. decussata*. *Distorsio clathrata* (LAMARCK, 1816:pl. 413, fig. 4a, b), on the other hand, has a Pliocene presence in the Caribbean region (WOODRING, 1928:pl. 19, figs. 2, 3; RUTSCH, 1930:pl. 17, figs. 4, 5). It is also known from the Ecuadorian Pliocene (OLSSON, 1964:174, pl. 30, figs. 1–1b), although it did not survive in the Pacific after the closure of the Mid-American seaways.

Both *Distorsio minoruohnishii* and *D. jenniernestae* may have evolved from the Neogene *D. constricta* stock in the equatorial waters of Central America, or from some yet unrecognized stocks. On the other hand, the relationship of these two species with the Indo-Pacific *D. habei* LEWIS (1972:38, figs. 38, 39) is not clear. Until recently, *D. habei* was recognized as a geographical subspecies of *D. constricta* (cf. BEU, 1985:62; LEWIS, 1972:44, figs. 38–39; EMERSON, 1991:68). Perhaps genetic differences determined by molecular studies could shed more light on the relationships of these taxa.

Distorsio (Distorsio) decussata
(Valenciennes, 1832)

(Figures 21, 22)

Tritonium decussatum VALENCIENNES, 1832:306; EMERSON & PUFFER, 1953:99; KILIAS, 1973:203, in part, name only, excluding references to *Distorsio constricta*.

Distorsio decussatus Valenciennes: PILSBRY & OLSSON, 1941:40, pl. 5, fig. 9; HERTLEIN & STRONG, 1955:265, 266; EMERSON & OLD, 1963:27, fig. 25; KEEN, 1971:508, fig. 963; LEWIS, 1972:43, figs. 36, 37; PARTH, 1991a:11, 2nd row, four specimens illustrated.

Type locality: "Habitat cum praecedente [*Tritonium hemastoma*] ad portum Acapulco," Guerrero, Mexico.

Type depository: There are no specimens of this taxon among Valenciennes' type material in the Muséum National d'Histoire Naturelle, Paris. The types are presumed to be lost (A. Beu, *in litt.*, to W. K. Emerson, 25 October 1991). In the absence of any known type specimens, we here designate as the neotype of *D. decussata* (Valenciennes, 1832) a specimen dredged from the Arena Bank, Baja California Sur, Mexico (23°29'N, 109°25'W) in 82 m (AMNH 85335, see Figures 21, 22).

Distribution: Golfo de California, Mexico to Manta, Ecuador (HERTLEIN & STRONG, 1955).

Material examined: 34 lots in the AMNH collection, from Mexico, Panama, Colombia, and Ecuador.

Remarks: VALENCIENNES (1832:306) did not illustrate his new species from Acapulco, Mexico. He stated *Distorsio decussata* was intermediate in characters between *D. anus* and *D. clathrata*. He compared his species with *D. clathrata*, noting differences in the anal sinus and the columellar plicae. He described a small (H = 54 mm), weakly distorted, white shell with reddish spots on the parietal shield, and he noted the presence of uneven labial plicae of which the third plica was the largest. The siphonal canal was described as elongated and thin edged. For the purpose of nomenclatural stability, we have selected a neotype (see above).

This is the largest of the four west American species, attaining more than 85 mm in length (AMNH 226426; dredged off Veraguas, Panama, J. Ernest, 1991). The weak distortion, long siphonal canal, deeply grooved columellar notch, and very large third plica on the inner edge of outer lip serve to characterize this species (Table 1). The periostracum on the outer surface is dark brown and covers a tannish basal layer (cf. LEWIS, 1972:37). A delicate prominent single hair occurs on the nodules formed at the intersection of the axial and spiral cords.

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A Re-evaluation of the Ontogeny of *Cabestana spengleri* (Perry, 1811) (Gastropoda: Tonnoidea: Ranellidae)

by

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Abstract. The egg mass, hatching, and early veliger of *Cabestana spengleri* are described. The statement by ANDERSON (1959) that *C. spengleri* has direct development is not confirmed and the contradicting data of KESTEVEN (1901), who figured a larval shell, are confirmed. *Cabestana spengleri* has a planktotrophic larva that lives long enough to cross the Tasmanian Sea.

INTRODUCTION

WILSON & GILLET (1971) wrote: "However at least one species, *Cabestana spengleri*, has been reported to have direct development (ANDERSON, 1959)." They refer to the Ranellidae Gray, 1854 (= Cymatiidae Iredale, 1913). HOUBRICK & FRETTER (1969) also cite Anderson's results: "ANDERSON (1959) [reported] the egg capsules and enclosed veligers of *Cymatilesta spengleri* (Perry), a species with no free larva, from Queensland." KILIAS (1973) documented some of Anderson's figures.

Anderson did not mention the publication of KESTEVEN (1901), who figured the protoconch of *Cabestana spengleri* (Figure 7). The drawing shows a shell that resembles a typical protoconch (for figures of ranellid protoconchs see as examples BANDEL, 1975, 1981, 1991; BEU, 1978, 1986, 1988; BEU & KAY, 1988; BEU & KNUDSEN, 1987; CLENCH & TURNER, 1957; KESTEVEN, 1901, 1902; LAURSEN, 1981; LEWIS, 1974; PILKINGTON, 1974; RICHTER, 1984; SCHELTENA, 1966, 1971; WARÉN & BOUCHET, 1990) of a ranellid gastropod with a planktotrophic veliger phase. Although discussing larval strategies and protoconchs of the Tonnoidea, WARÉN & BOUCHET (1990) did not mention the "problem" concerning *C. spengleri*. If Anderson was right in maintaining that *C. spengleri* has direct development, it would not be possible to differentiate protoconchs of species with planktotrophic larvae from those not having this phase in their ontogeny. Consequently a short review of Anderson's work was necessary.

MATERIALS AND METHODS

Specimens of *Cabestana spengleri* and their egg masses were collected during the first week of December 1990 at Long

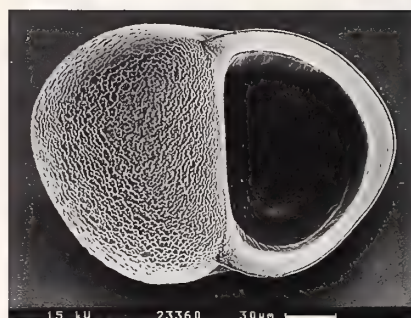
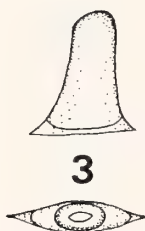
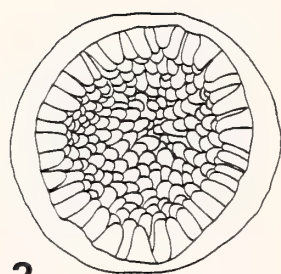
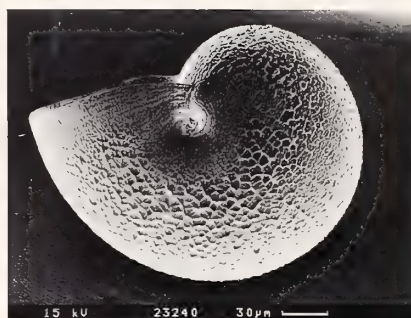
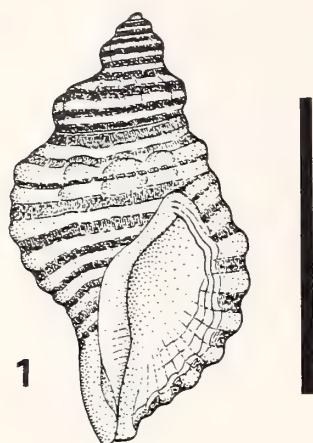
Reef (northern Sydney, Australia) and then transported to the Division of Invertebrate Zoology, Australian Museum. The spawn was kept in 10-L tanks. When hatching started the spawn was moved daily into a new tank in order to keep the older veligers separate from the younger ones. The veligers were observed with the aid of a light microscope. Drawings were made from different stages in different situations. Every day a few hundred veligers were fixed in 70% ethanol. Investigations on living specimens had to be terminated during the fifth day after hatching since facilities were not available to rear the veligers for a longer period of time.

The number of egg capsules in a spawn was counted, and ten capsules were removed from one egg mass. Each of these capsules was opened into a dish. The embryos were washed with ethanol and dispersed on the counting frame on the bottom of the dish. When the ethanol had evaporated, the embryos were counted. The different stages of veligers fixed in alcohol were measured (about 20 shells represented every day of development) and photographed with the aid of an SEM (Geological-Palaeontological Institut, Hamburg).

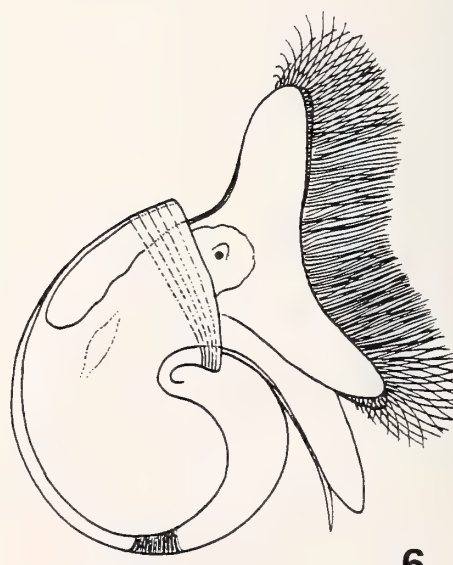
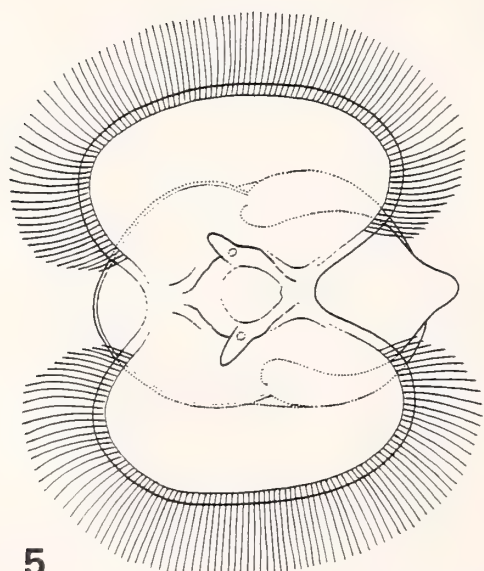
The material is deposited under M 1035 at the Zoological Institut and Museum (University of Hamburg).

RESULTS

Cabestana spengleri (Figure 1) lives mainly on rocks exposed at low tide (LAXTON, 1969; personal observations) but also occurs down to 30 m depth (POWELL, 1979). *Cabestana spengleri* feeds on ascidians (LAXTON, 1969; personal observations). Spawning and breeding occurs from October to December (personal communication from Phil



4b



Colman; personal observations). This period applies only to the Long Reef region because water temperature influences the start of the breeding season. For example, at Leigh (northern New Zealand), females of *C. spengleri* spawn and breed from November to January (LAXTON, 1969).

The egg mass of *Cabestana spengleri* (Figure 2) resembles a bowl (see also SIMROTH, 1907; LAXTON, 1969; DOUGLAS, 1985—not correct). The size is proportional to the diameter of the shell aperture of the snail that produces the egg mass (LAXTON, 1969; personal observations). ANDERSON (1959) figured a specimen of *C. spengleri* together with an egg mass, but his photographs show a spawn that is too large for the specimen. Anderson assumed that the egg mass belonged to *C. spengleri* because the gastropod was attached to it. Actually *C. spengleri* remains on the spawn until the embryos hatch (LAXTON, 1969; personal observations), a behavior that seems typical for the whole family (BANDEL, 1976; BANDEL & WEDLER, 1987). Anderson cautiously wrote that he suspected the collected egg masses belonged to this species.

The spawn of *Cabestana spengleri* contains between 200 and 350 egg capsules (LAXTON, 1968). The number of egg capsules is not proportional to the diameter of the spawn (LAXTON, 1969). The egg capsule (Figure 3) of a spawn containing 224 capsules holds an average of approximately 4000 embryos, with a range of 3000 to 5000. These numbers indicate that a single spawn of *C. spengleri* houses about one million embryos.

When hatching commences, an average of one to two veligers per second leave the egg mass, since it takes about one week until all egg capsules are empty. When the veligers start their planktonic life, the shell has reached nearly one whorl. This part of the whorl is defined as the embryonic shell. Growth can be seen in Figure 4a. This veliger was swimming free for three days. The beginning of growth lines marks the time of hatching. The diameter of the embryonic shell varies around 200 μm . The shape is slightly asymmetrical (Figure 4b), and the reticulate sculpture seems to be typical for the Tonnoidea (BANDEL, 1975). The velum (Figure 5) is bilobate. Each lobe is set with about one hundred 50- μm long cilia. The shape of the foot is typical for the Tonnoidea (PILKINGTON, 1976). The foot is also ciliated, but the cilia are much shorter

than those of the velum. The head possesses two tentacles with eyes at their base.

A veliger can reach a speed of 5 mm/sec, which is equivalent to traveling 25 times its own length in one second. Figure 6 shows a two-day-old veliger that has slightly retracted its velum. The visceral mass is rounded and still full of yolk. The amount of yolk quickly decreases during the following days of development. Between the apical part of the visceral mass and the shell, the retractor muscle is visible. The heart is situated beneath the rear end of the pallial cavity. The head is less developed compared with that of a veliger one day older (*i.e.*, the tentacles are shorter). The foot bears an operculum that is functional (see also Figure 4b).

The completed protoconch (Figures 7, 8) has more than four whorls.

DISCUSSION

The distribution of *Cabestana spengleri* includes the southern part of eastern Australia as far north as southern Queensland, the coasts of Victoria and South Australia, Tasmania (WILSON & GILLET, 1971) and New Zealand and "surrounding" islands (POWELL, 1979), from the northern Three Kings Islands to southern Stewart Island, and the Chatham Islands.

For a gastropod with direct development not known to live deeper than 30 m, it would be difficult to explain such a distribution, on both sides of the Tasman Sea, with populations separated by up to 2000 km of deep ocean. Assuming that the planktotrophic veliger grows as fast as it did during the first days of development (see above) it would need about three months to construct three whorls of larval shell. This is of course a daring assumption because nothing is known about the special circumstances of the veliger on its journey; however, other members of the Ranellidae (SCHELTEMA, 1966, 1971) have larval lives of three months to a year (maybe more), and show that the possibility exists.

It seems likely that ANDERSON (1959) either described the early life history of some other gastropod in the egg mass on which *Cabestana spengleri* happened to be found, or the development within the egg mass of *C. spengleri* was abnormal in this case (perhaps caused by poor tank con-

Explanation of Figures 1 to 6

Figure 1. The teleoconch of *Cabestana spengleri*. Scale bar: 10 cm.

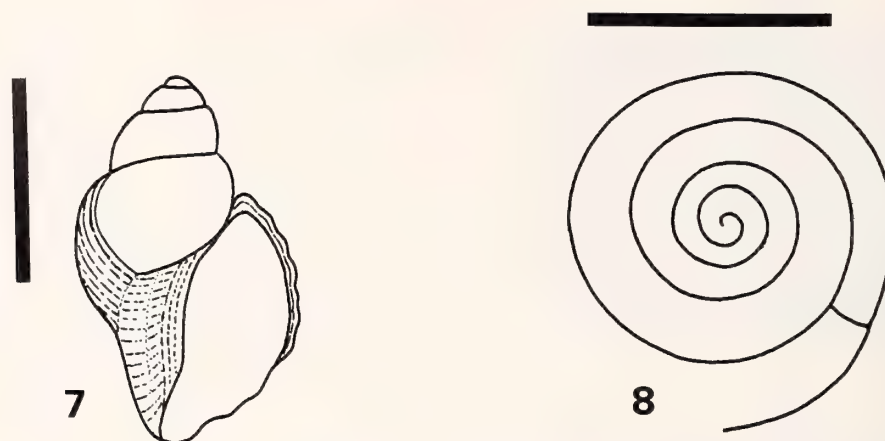
Figure 2. The spawn of *C. spengleri* in dorsal view and the outline of the side view. Scale bar: 2.5 cm.

Figure 3. The egg capsule of *C. spengleri*, showing the opening on top through which the veligers hatch. Scale bar: 1 cm.

Figure 4a, b. Shell of a three-day-old veliger of *C. spengleri*.

Figure 5. Three-day-old veliger of *C. spengleri*, anterior view. Scale bar: 0.2 mm.

Figure 6. Two-day-old veliger of *C. spengleri*, lateral view. Scale bar: 0.2 mm.



Explanation of Figures 7 and 8

Figure 7. Juvenile *Cabestana spengleri* showing the protoconch, drawn after KESTEVEN (1901). Scale bar: 3 mm.

Figure 8. Apical view of the protoconch of a juvenile *C. spengleri*, showing the number of whorls (drawn from an SEM photo). Scale bar: 1.5 mm.

ditions). The second possibility could be supported by Anderson's figures of the embryo, which show unusual characters (*e.g.*, the huge "oral hood").

Of great importance is the fact that a gastropod with a protoconch, indicating a planktotrophic veliger (KESTEVEN, 1901), actually has this stage in its ontogeny. *Galeodea* (= *Cassidaria*) *echinophora* (Linnaeus, 1758) is one member of the Tonnoidea in which direct development is confirmed (FIORONI, 1966) and its protoconch consists of not more than one whorl (ABBOTT, 1968; WARÉN & BOUCHET, 1990).

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The Fossil Land Snail *Helix leidy* Hall & Meek, 1855, a Member of a New Genus of Humboldtianidae (Gastropoda: Pulmonata)

by

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Abstract. The latest Eocene to earliest Oligocene terrestrial snail *Helix leidy* Hall & Meek, 1855, is redescribed, based on a re-examination of the holotype and well-preserved specimens from east-central Wyoming. Much early identification of the species was based on a specimen erroneously accepted as the holotype. *Helix leidy* is designated the type species of a new genus of Humboldtianidae, *Skinnerelix*. *Skinnerelix* differs from the extant genus *Humboldtiana* von Ihering, 1892, in having a larger number of whorls, a higher spire, and a distinctly everted peristome with a slight constriction behind the basal lip. *Humboldtiana* may have originated from *Skinnerelix* progenetically. (Humboldtianidae, Helicidae) probably represents a Laurasian, cratonal clade with a history long independent of the Gondwanan, accretional clade consisting of (Helminthoglyptidae, Bradybaenidae, Xanthonychidae).

INTRODUCTION

Helix leidy Hall & Meek, 1855, was the first fossil land snail species described from the western United States and has become one of the most widely cited but poorly understood species of middle Tertiary land snails. The holotype of *Helix leidy* was collected in 1853 by F. B. Meek and F. V. Hayden in the badlands of the White River "series" in the Nebraska Territory (now western South Dakota). Subsequent to its description by HALL & MEEK (1855), classification and identification of the species were confused by the designation of an erroneous "holotype" and widespread use of the name for any large helicoid snail fossils from rocks of medial Tertiary age in the mid-con-

tinental region. Re-examination of the holotype and discovery of well-preserved specimens in east-central Wyoming (Figures 1-7) indicate that *Helix leidy* is a member of a new genus of the Humboldtianidae. Its presence in latest Eocene and earliest Oligocene rocks of the Great Plains and central Rocky Mountains (Figure 8) has significant implications for biogeographic hypotheses concerning Humboldtianidae and Helicoidea.

The following abbreviations are used: AMNH, American Museum of Natural History, New York; UCM, University of Colorado Museum, Boulder; USNM, National Museum of Natural History, Washington, D.C.; USGS, United States Geological Survey.



Explanations of Figures 1 to 7

Figures 1–7: *Skinnerelix leidy* (Hall & Meek, 1855).

Figures 1–3. Holotype, AMNH 11174/1, from the Scenic Member, Brule Formation, White River Group (lower Oligocene), near Scenic, Pennington County, South Dakota. Side, apertural, and oblique spire view; specimen coated for photographing; height 24.3 mm. Arrow on Figure 3 indicates point marked by arrow in Figure 9.

Figures 4–7. Figured specimen, UCM 30732, from Chadron Member, White River Formation (upper Eocene), near Douglas, Converse County, Wyoming (UCM loc. 90004). Apertural, side, spire, and basal views; specimen coated for photographing; maximum diameter 31.6 mm.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Subclass Pulmonata

Superorder Stylommatophora

Order Sigmurethra

Superfamily HELICOIDEA

Family HUMBOLDTIANIDAE

Skinnerelix Evanoff & Roth, gen. nov.**Type species:** *Helix leidy* Hall & Meek, 1855.

Generic diagnosis: Shell large (adult shells larger than 2 cm in maximum diameter); globose-conic; height to maximum diameter ratio greater than 0.8; embryonic shell smooth, consisting of first 1.2 whorls; neanic sculpture of growth rugae and coarse, somewhat crude granulation arranged in diagonal rows; last whorl broadly rounded, tumid, descending, constricted basally just behind lip; peristome flaring, narrowly turned outward, reflected at base and columella; base narrowly, obliquely perforate.

Remarks: Several features indicate assignment of *Skinnerelix* to the Humboldtianidae. It shares the following features with the extant genus *Humboldtiana* von Ihering, 1892: a globose-conic, narrowly perforate shell; fewer than five whorls; an embryonic shell of 1.2 whorls; coarse, rather crude granulation; and a tumid, descending last whorl. The granulation of *Skinnerelix* consists of close-set, round to ovate granules in diagonal rows relative to the growth lines and collabral rugae (Figures 9–11). Granulation of this type occurs in many species of *Humboldtiana*, including *H. chisosensis* Pilsbry, 1927, *H. globosa* Burch & Thompson, 1957, *H. palmeri* Clench & Rehder, 1930 (Figure 12), and *H. texana* Pilsbry, 1927. It differs from the fine, regular, fabric-like granulation found in some species of the helminthoglyptid genus *Xerarionta* Pilsbry, 1913 (e.g., *Xerarionta redimita* (Binney, 1858); see ROTH, 1984:fig. 32). In some species of *Helminthoglypta* Ancy, 1895, a still different form of granulation occurs in which close-set collabral rugae are cut into rows of elongate granules by incised spiral striae or shallow, forwardly descending sulci.

Skinnerelix differs from *Humboldtiana* in having more inflated whorls, a slightly larger number of whorls (more than 4.1 whorls compared with typically fewer than 4.1 whorls for *Humboldtiana*), a higher spire, and a distinctly everted peristome with a slight constriction just behind the basal lip. Features of adult *Humboldtiana* shells, such as the lack of an everted peristome and the small number of whorls, are characteristics of *Skinnerelix* shells that have not attained their full, adult growth, and suggest that *Humboldtiana* may have originated from a *Skinnerelix*-like ancestor by a process of progenesis.

Skinnerelix occurs in upper Eocene and lower Oligocene rocks of the Big Badlands of South Dakota, the Pine

Ridge of northwestern Nebraska, near Douglas, Wyoming (all, *S. leidy*), and in the Keetley Volcanics, near Peoa, northeastern Utah (*S. sp.*, cf. *S. leidy*) (Figure 8). *Humboldtiana* is predominantly a genus of the Mexican Plateau (Figure 13), ranging from Mexico City in the south to the Guadalupe Mountains of New Mexico in the north (BURCH & THOMPSON, 1957; BEQUAERT & MILLER, 1973).

We have examined the holotype of *Humboldtiana? tuckerae* Mansfield, 1937, USNM 495934 (not 4959340, as originally published), from the Tampa Limestone, upper Oligocene of Florida. The outer lip is smoothly rolled outward a short distance, with a small internal varix that is not reflected externally in any constriction of the whorl. The inner lip is triangularly dilated over the umbilicus leaving an open, tubular, oblique perforation. Behind the aperture, the body whorl does not depart from the prior whorl trajectory and in fact descends very little.

The embryonic sculpture consists of low, obscure vermiculation overlain by widely spaced, round, flat-topped papillae. The post-embryonic sculpture consists of indistinct collabral ribs, slightly nodulose, and separated by interspaces of about the same width; small patches of short, axially elongated indentations are present. No sculpture of close-set, round to ovate granules in diagonal rows is present.

On the basis of these observations, we do not consider *Humboldtiana? tuckerae* assignable to *Skinnerelix*. F. G. Thompson (in UNDERWOOD & WILSON, 1974) referred *H.? tuckerae* to the genus *Cepolis* Montfort, 1810.

UNDERWOOD & WILSON (1974) reported an unnamed species of *Humboldtiana* from the Garren Group, Hudspeth County, Texas, found in association with Chadronian Age land mammals in strata radioisotopically dated at 39–36 Ma. The specimens are crushed and distorted, with little shell surface and no adult apertures preserved. They are probably juvenile. The largest is 17+ mm in diameter, with about 3.3 whorls. Without better material, it is not possible to state whether these specimens represent *Humboldtiana*, *Skinnerelix*, *Xerarionta waltmilleri* Roth, 1984, as suggested by ROTH (1984), or another taxon.

Etymology: The name *Skinnerelix* combines the Greek word *helix*, a spiral, hence a snail, and the name of the late Dr. Morris Skinner, collector for the American Museum of Natural History. Skinner's collections of White River land snails for the AMNH are the largest in the country, and his stratigraphic studies are the basis for many of our modern concepts of White River correlations. The gender of *Skinnerelix* is feminine.

Skinnerelix leidy (Hall & Meek, 1855)

(Figures 1–7, 9–11)

Helix leidy HALL & MEEK, 1855:394, pl. 3, fig. 12a, b;
MEEK, 1876:604–605, pl. 45, fig. 7a, b.

?*Helix leidy* Hall & Meek: WHITE, 1877:211 (in part), pl. 21, fig. 3a, b.

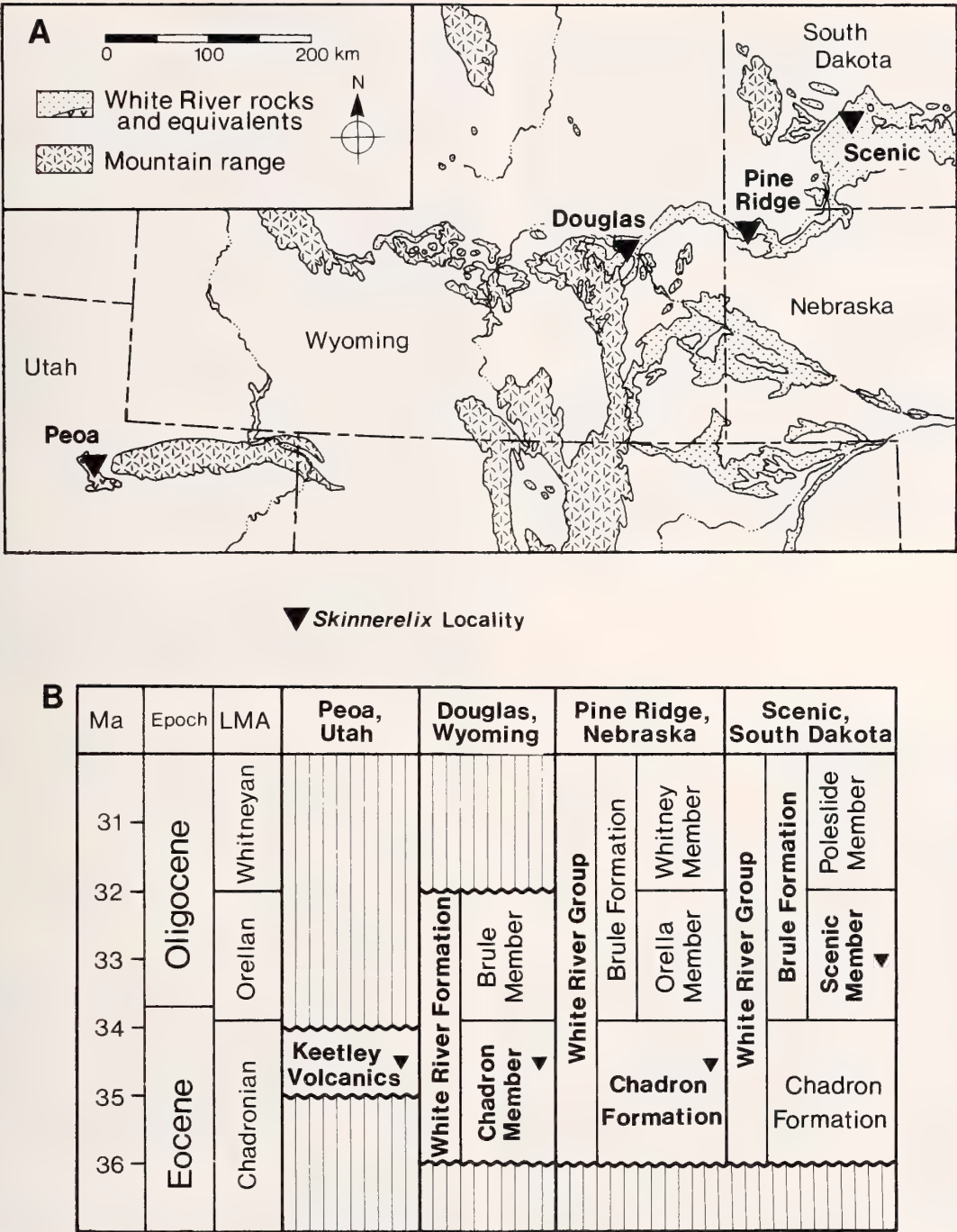


Figure 8

Distribution (A) and chronostratigraphy (B) of *Skinnerelix* localities.

Helix (Arianta?) leidyi Hall & Meek: WHITE, 1883:455, 475, pl. 32, figs. 32, 33.

[*Polygyra*] *leidyi* (Hall & Meek): HANNA, 1920:9.

Polygyra leidyi (Hall & Meek): TOEPELMAN, 1922:65.

Pseudolisinos leidyi (Hall & Meek): WENZ, 1923:116.

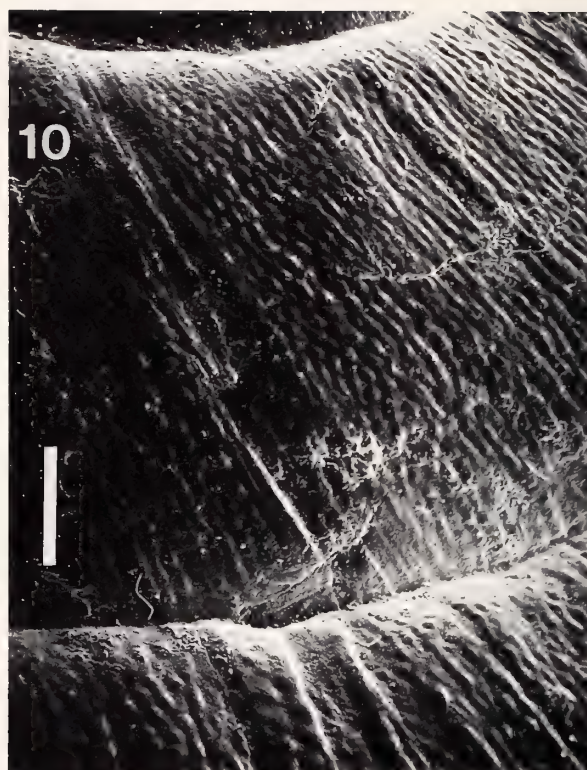
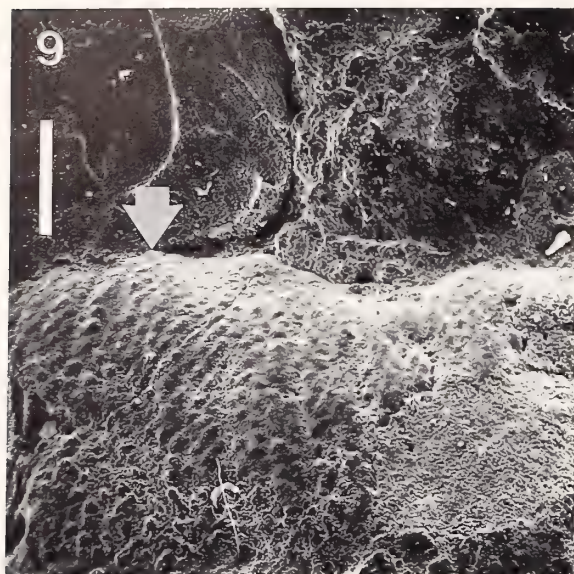
Glypterpes leidyi (Hall & Meek): ZILCH, 1960:655.

Non Helix leidyi Hall & Meek: WHITE, 1877:211 (in part),

pl. 21, fig. 3c; COCKERELL & HENDERSON, 1912:232, pl. 22, figs. 1-3; PAMPE, 1974:292, pl. 1, figs. 1-10.

Non Mesodon leidyi (Hall & Meek): Russell, in GOLDICH & ELMS, 1949:1145.

Diagnosis: Shell large, spire broad, whorls inflated and shouldered; embryonic shell smooth, regularly increasing



Explanation of Figures 9 to 12

Figure 9. *Skinnerelix leidy*, holotype, AMNH 11174/1. SEM photograph of diagonal granular microsculpture on apical side of last whorl, just before crushed area (see arrow on Figure 3). Bar is 1 mm long; epoxy cast of specimen coated for photographing.

Figure 10. *Skinnerelix leidy*, figured specimen, UCM 30732. SEM photograph of diagonal granular microsculpture on last and penultimate whorls, about 0.2 whorls behind aperture. Bar is 1 mm long; epoxy cast of specimen coated for photographing.

in diameter after nucleus; sculpture of coarse granulations arranged in diagonal rows extending from adapical side to base; last whorl tumid, gradually descending in last 0.2 to 0.25 whorl.

Original description: "Shell subglobose, wider than long; spire elevated; volutions four or five, last one large and ventricose; suture distinct; surface unknown; aperture unknown; outer lip reflected; umbilicus small, or perhaps closed. The last volution .65 of whole length. The aperture is ovate, subangular behind" (HALL & MEEK, 1855:394, 411).

Description of holotype: Shell large, globose-conic, very narrowly perforate. Spire slightly convex in profile, with apical angle of 121°, sutures moderately impressed, whorls shouldered. Sculpture on penultimate and last whorls including retractive, moderately prominent growth lines and granulations arranged in diagonal rows. Last whorl tumid, rounded, descending in last 0.2 whorl; base slightly constricted upward behind lip. Peristome everted; columellar lip recurved, dilated over umbilical perforation.

Type material: Holotype: AMNH 11174/1 (James Hall number 5547/1). South Dakota, Pennington County: near the head of Bear Creek, Mauvais Terres, turtle and bone bed (HALL & MEEK, 1855:394) collected by Meek and Hayden in 1853. About E ½, T. 3 S., R. 13 E. (HARTMAN, 1984:907); from the Scenic Member, Brule Formation, White River Group; Orellan Land Mammal Age.

Referred material (all near Douglas, Converse County, Wyoming): UCM 30732 (figured), UCM locality 90004; UCM 30753, UCM locality 87063; UCM 30733, UCM locality 90004; UCM 30734, UCM locality 90005; UCM 30735, UCM locality 83235. Occurring 69.8 to 62.2 m below the top of the Chadron Member, White River Formation; Chadronian Land Mammal Age.

Additional description of referred material: The referred specimens from the Douglas area, Wyoming, are similar in size and identical in shape, sculpture of the penultimate and last whorls, and peristome morphology to the holotype, but are better preserved. The ratio of spire height to shell height in the referred specimens ranges from 0.25 to 0.31 (mean 0.27). The embryonic shells of the referred specimens consist of 1.2 smooth whorls, separated from the neanic whorls by a slight constriction, increasing whorl translation rate, and the beginning of distinct growth

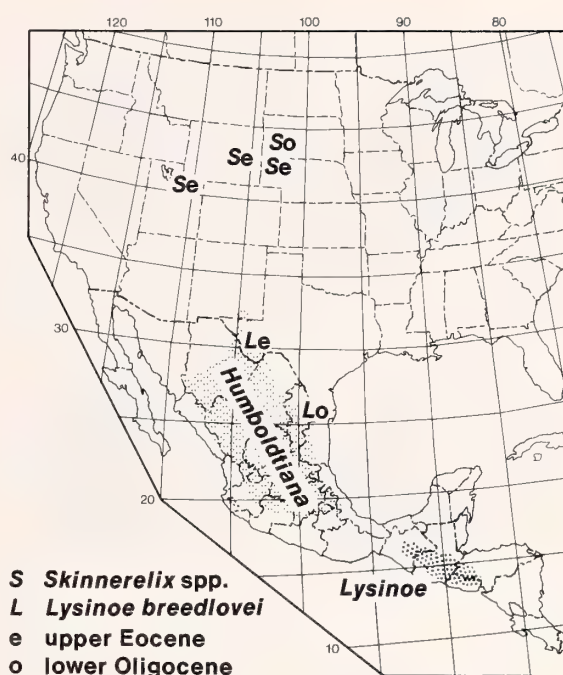


Figure 13

Distributions of modern and fossil species of *Skinnerelix*, *Lysinoe*, and *Humboldtiana*. *Lysinoe* distribution from DALL (1897), THOMPSON (1963), ROTH (1984), and unpublished museum records. *Humboldtiana* distribution from PILSBRY (1927, 1939, 1948), SOLEM (1954, 1955), BURCH & THOMPSON (1957), and BEQUAERT & MILLER (1973).

lines. The nucleus has a typical width of 0.5 mm; the embryonic shell is not distinctly inflated after the nucleus. The neanic whorls are rounded, with granulations starting at about whorl 2, initially weak, becoming prominent after 2.75 whorls. The last whorl gradually descends in the last 0.2 to 0.25 whorl, with the lower palatal limb becoming increasingly expanded. The adapical and basal sides are slightly constricted just before the lip. Granulations are coarse and prominent on the adapical and palatal sides, weak on the base, and absent in the shallow umbilical area. The growth lines coalesce to form weak collabral rugae on the last whorl. The aperture is rounded, ovate-lunate; the outer lip is narrowly expanded on the adapical and marginal sides, recurved basally. The columellar lip is dilated and reflected. The parietal wall has a simple callus pad.

Figure 11. *Skinnerelix leidy*, figured specimen, UCM 30732. SEM photograph of protoconch and coarse granular microsculpture on whorls 2 and 3. Bar is 1 mm long; epoxy cast of specimen coated for photographing.

Figure 12. *Humboldtiana palmeri* Clench & Rehder, 1930, Recent, USNM 408371/1, Davis Mountains, Jeff Davis County, Texas. SEM photograph of protoconch and coarse granular microsculpture arranged in diagonal rows relative to growth lines. Bar is 1 mm long; specimen coated for photographing.

A. Hall and Meek (1855)



B. Meek (1876)

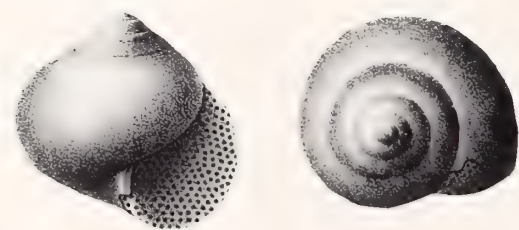


Figure 14

Original lithograph illustrations of *Helix leidyi*. A. Apertural and side views of holotype of *Helix leidyi* (AMNH 111774/1) as illustrated by HALL & MEEK (1855:pl. 3, fig. 12a, b). B. Apertural and spire views of *Helix leidyi*(?) (USNM 2102) as illustrated by MEEK (1876:pl. 45, fig. 7a, b). Specimen 26.0 mm high, maximum diameter 26.2 mm. Stippled areas represent parts of the specimen reconstructed with beeswax.

Remarks: “*Helix*” *leidyi* has been the subject of taxonomic confusion. The holotype (AMNH 111774/1) (Figures 1–3), illustrated by HALL & MEEK (1855; their illustration reproduced here as Figure 14A), is mostly an internal mold of an adult shell, with the embryonic shell and most of the spire poorly preserved. The adapical and marginal sides of the last 0.25 whorl are crushed, but shell is preserved on the adapical side of the last whorl just before the crushed area, and above this on the penultimate whorl. Despite preservational defects, the type specimen has enough features to distinguish the species from other Tertiary helicoids.

In the National Museum of Natural History is a specimen of “*Helix*” *leidyi* (USNM 2102) which is labeled “holotype,” but is not the specimen illustrated by HALL & MEEK (1855). This specimen is an internal mold with no original shell and has been so over-prepared that the surface of the spire has been sculpted. The last 0.2 whorl was reconstructed with beeswax (Figure 14B). The wax reconstruction does not represent the descent of the last whorl, indicated by a slight downward reflection of the suture, and does not have a reflected lip, which is clearly preserved on the actual holotype. USNM 2102 was first illustrated by MEEK (1876) without reference to the reconstructed aperture. Unfortunately, this specimen is the one regarded by WHITE (1883), COCKERELL (1915), and subsequent workers as the type specimen of “*Helix*” *leidyi*,

producing confusion in the taxonomy of the species. For example, COCKERELL (1915) could not distinguish this specimen from species of *Glypterpes* Pilsbry, 1892. On this basis, WENZ (1923) subsequently included “*H.*” *leidyi* in his genus *Pseudolisinoe*, a junior synonym of *Gypterpes*.

The specimens referred to as “*Helix leidyi*” by WHITE (1877) include one specimen (USNM 484) that may be assignable to *Skinnerelix* but has been greatly modified by preparation, and another (USNM 829) that is openly umbilicate and has a dome-shaped shell, features not found in *S. leidyi*.

COCKERELL & HENDERSON (1912:pl. 22, figs. 1–3) illustrated three specimens identified as “*Helix leidyi*.” One of these (AMNH 43562) has a depressed spire and a distinct umbilicus, and is not a species of *Skinnerelix*. It is probably a member of an undescribed taxon of Whitneyan helicoids characterized by a moderately depressed spire and shouldered early whorls. The other two specimens (AMNH 43561, 43563) are poorly preserved internal molds and not identifiable.

PAMPE (1974) discussed and illustrated specimens he identified as “*Helix leidyi*” from the Eocene and Oligocene of west Texas, but ROTH (1984) reassigned them to *Lysinoe breedlovei* Roth, 1984, and *Xerarionta waltmilleri* Roth, 1984.

The systematic position of “*Helix*” *leidyi* has long been uncertain. Early workers (HALL & MEEK, 1855; MEEK, 1876; WHITE, 1883; COCKERELL, 1915) placed all large fossil helicoid-shaped snail shells from North America in the Helicidae, under the genera *Helix* Linnaeus, 1758, or *Arianta* Leach, 1831. HENDERSON (1935) and LA ROCQUE (1960) continued to refer to fossil helicoids as *Helix*? or “*Helix*,” stressing the difficulties in determining generic position from shell features alone. The family Helicidae is now considered to be native to Eurasia and North Africa. Species of *Helix* and *Arianta* have domed spires with weakly impressed sutures, tumid embryonic shells, and sculpture of spiral striations and malleations, features not found in *Skinnerelix*.

HANNA (1920) referred “*Helix*” *leidyi* to the Polygyridae (although not explicitly to any one genus) because of its similarity to *Polygyra martini* Hanna, 1920, of the John Day Formation in Oregon. TOEPELMAN (1922), assigned *Skinnerelix leidyi* to *Polygyra* Say, 1818. Russell (in GOLDICH & ELMS, 1949) placed the species in the polygyrid genus *Mesodon* Rafinesque, 1821. Globose-conic polygyrids without apertural barriers, such as certain species of *Mesodon*, *Neohelix* von Ihering, 1892, and *Allogona* Pilsbry, 1939, have one or more of the following features: a domed spire, spiral striae, distinct radial ridges or malleations, a broadly expanded peristome, an ovate-lunate aperture, and a strong basal preapertural constriction that causes the basal wall to rise adapically. *Skinnerelix leidyi* has none of these features. Furthermore, ROTH (1987) demonstrated that *P. martini* is assignable to *Helminthoglypta*, not to the Polygyridae. *Helminthoglypta martini*

differs from *Skinnerelix leidy* by being more widely umbilicate and having sculpture of retractive slanting riblets, spiral striae, and malleation.

COCKERELL (1915), examining figured specimens of *Skinnerelix leidy* at the National Museum of Natural History, decided that the species was not generically distinguishable from the Eocene taxa "*Helix veterna* Meek & Hayden, 1861, "*Helix*" *riparia* White, 1876, and "*Helix*" *veterna veternior* Cockerell, 1915. Following COCKERELL (1915) in this respect, WENZ (1923) grouped these taxa into a new genus, *Pseudolisinoe*, with "*H.*" *veterna* as the type species. (*Pseudolisinoe* is an objective synonym of *Glypterpes* Pilsbry, 1892, type species "*H.*" *veterna*.) From an examination of the holotypes of *Glypterpes veterna* and *G. riparia*, we regard *Skinnerelix* and *Glypterpes* as distinct. Species of *Glypterpes* have more conical shells, less inflated whorls, spiral striation instead of granulation, and less everted peristomes than species of *Skinnerelix*.

The modern species of *Humboldtiana* that most closely resembles *Skinnerelix leidy* is *H. globosa* from the state of Vera Cruz, Mexico. Both species have highly inflated, shouldered whorls, smooth embryonic shells, and granulations arranged in diagonal rows relative to the growth rugae; both are of similar size.

Distribution and stratigraphic range: Scenic Member, Brule Formation, White River Group, Big Badlands, Pennington County, South Dakota (type locality); Orellan Land Mammal Age. Chadron Formation, White River Group, within 6 m below the top of the Chadron, Sioux County, Nebraska (USGS Cenozoic localities 20025, 22672); late Chadronian Land Mammal Age. Chadron Member, White River Formation, between 71.3 to 9.0 m below the top of the Chadron Member near Douglas, Wyoming (EVANOFF, 1990); late Chadronian Land Mammal Age. The species ranges from the latest Eocene to earliest Oligocene (late Chadronian to Orellan land mammal ages). *Skinnerelix leidy* is common and the most obvious land snail fossil of the Chadron Member in the Douglas area. The specimens of *Skinnerelix* sp., cf. *S. leidy* from the upper Eocene Keetley Volcanics (dated between 35 and 34 Ma; HINTZE, 1988) near Peoa, Summit County, Utah (USGS Cenozoic locality 23306) are too incomplete to be referred to *S. leidy* with certainty.

BIOGEOGRAPHIC AND PALEOCLIMATIC SIGNIFICANCE

Leaving out the problematic *Humboldtiana* of UNDERWOOD & WILSON (1974), the fossil record of Humboldtianidae consists of the occurrences of *Skinnerelix* described above and *Lysinoe breedlovei* Roth, 1984, from the upper Eocene of Trans-Pecos Texas and the lower Oligocene of Nuevo León, Mexico. In western Texas, *L. breedlovei* ranges from the lower part of the Devils Graveyard Formation (associated with the Uintan Whistler Squat local fauna) to

the Bandera Mesa Member of the Devils Graveyard Formation (associated with the early Chadronian Coffee Cup local fauna) (ROTH, 1984). All of these occurrences are older than the occurrences of *Skinnerelix* in the central Rocky Mountains and western Great Plains. *Lysinoe breedlovei* also occurs in lower Oligocene rocks of Nuevo León, Mexico (ROTH, 1984) that are equivalent to the Vicksburg Group (GARDNER, 1945), and about the same age as the Orellan Land Mammal Age (SWISHER & PROTHERO, 1990). By the late Eocene, at least two humboldtianid clades, that of *Lysinoe* and that of (*Humboldtiana*, *Skinnerelix*), were differentiated.

Species of *Lysinoe* now live predominantly south of the range of *Humboldtiana* (Figure 13), and *Lysinoe breedlovei* also lived south of *Skinnerelix*. Both clades have shifted southward since the early Oligocene, but their relative distribution has remained constant.

Humboldtiana is a plausible environmental analogue to *Skinnerelix*. *Humboldtiana* ranges from Mexico City, Mexico, north to the Guadalupe Mountains in southeast New Mexico (Figure 13). It typically lives in a variety of substrates and woody vegetation, ranging from oak forests on limestone to high coniferous forests and mixed scattered woodlands on volcanic rocks (PILSBRY, 1939).

The climate in the range of *Humboldtiana* is subtropical, as defined by WOLFE (1979), with mean annual temperatures ranging from 13 to 21°C, and mean annual range of temperatures of 4–20°C (WERNSTEDT, 1972; WORLD METEOROLOGICAL ORGANIZATION, 1979). The presence of a land snail with subtropical affinities in the Rocky Mountains during the late Eocene is consistent with paleoclimatic interpretations based on the contemporaneous Florissant flora of Colorado (MACGINITIE, 1953).

The classification of the Helicoidea is in a state of flux (along with the rest of the Stylommatophora; see EMBERTON *et al.*, 1990), with opinions varying as to the relationships of the Humboldtianidae (*e.g.*, SCHILEYKO, 1978, 1979, 1991; NORDSIECK, 1987; TILLIER, 1989). A robust phylogenetic hypothesis is only now coming into place for the families of Helicoidea. (The wide-ranging paper of SCHILEYKO [1991] was published almost simultaneously with submission of the present paper; Roth [in preparation] has some rather different ideas about the genera of Helminthoglyptidae.) We regard the Humboldtianidae as a holophyletic group (*sensu* ASHLOCK, 1971), defined by the synapomorphies of a ring of nodular mucus glands surrounding the vagina at a single level, subtended by a ring of dart sacs sessile on the vagina.

In the view of SCHILEYKO (1978, 1991; personal communication to Roth, 1990) the condition of multiple mucus glands seated around the vagina and multiple sessile dart sacs is primitive relative to the smaller number of dart sacs (generally one) and more closely adjacent mucus glands found in Helicidae and in secondarily simplified genera such as *Leptarionta* Fischer & Crosse, 1872. It is morphologically closer to the hypothesized ancestral condition

in which the vaginal wall is extensively glandular and furnished with aragonitic spicules. The branching diagram of SCHILEYKO (1978:fig. 29) contains the clade ((Humboldtianidae, Helicidae), (Bradybaenidae, Helminthoglyptidae)); but the apomorphies (if any) defining the branch segments are not specified.

The cladogram of NORDSIECK (1987:fig. 30) includes Humboldtianidae within a heterogeneous family Xanthonychidae, separated from (Bradybaenidae, (Hygromiidae, Helicidae)) by the single, equivocal character of "dart glands [= mucus glands] not divided/divided." But in the bradybaenid genus *Aegista* Albers, 1850, for example, the mucus glands range from single to multiple, with variously one, two, or perhaps more insertions on the nebensack (AZUMA, 1982). In the helminthoglyptid genus *Micrarionta* Ancey, 1880, the glands are paired; in *Helminthoglypta* they could be said to be divided—there are two bulbous reservoirs leading into the common duct—even though they ultimately form a single membranous envelope around the dart apparatus.

MILLER & NARANJO-GARCÍA (1991) pointed out the correspondence between the distribution of the helicoid families Bradybaenidae, Helminthoglyptidae, and Xanthonychidae and the tectonically accreted terranes around the Pacific Rim. From this pattern they drew the conclusion that those families had a common ancestry on a Mesozoic Gondwanan land mass ("Pacifica"; see NUR & BEN-AVRAHAM, 1977; JONES *et al.*, 1982) and were dispersed passively to Asia and the Americas on rafting fragments of continental crust. They also noted that the distribution of Humboldtianidae does not correspond to any accretional realm, and therefore excluded the family from the above scenario. Humboldtianidae must have had a history independent from that of the "Pacifcan" families. Recognition of *Skinnerelix* as a genus of Humboldtianidae does not alter, and in fact reinforces, the model in this respect.

(Stratigraphic evidence is not well in accord with the "Pacifica" hypothesis for the origin of Helminthoglyptidae. The earliest fossil occurrences of *Helminthoglypta* (*H. bozemanensis* Roth, 1986), *Xerarionta* (*X. waltmilleri*), and *Polymita* (*P. texana* Roth, 1984) are an old continent, not accreted terrane. However, a thorough review of the fossil evidence, taking into account the uneven distribution of fossiliferous terrestrial deposits of critical ages, has yet to be made.)

Combining the phylogenetic hypothesis of SCHILEYKO (1978, 1991) and the historical zoogeography of MILLER & NARANJO-GARCÍA (1991) produces the following model: (Humboldtianidae, Helicidae) represents one (Laurasian, cratonal?) clade, with vicariance between the two families possibly related to the development of the Atlantic Ocean as a dispersal barrier. (Helminthoglyptidae, Bradybaenidae, Xanthonychidae) represents a second (Gondwanan, accretional?) clade, with possible vicariance related to the breakup of "Pacifica." Sympatry between members of these

two clades (*e.g.*, Recent *Sonorella* and *Humboldtiana* in northern Mexico, on old continent) must therefore be the result of dispersal (in this example, presumably of the helminthoglyptid into humboldtianid territory). Dispersal of the Gondwanan clade in North America must have proceeded from accreted to cratonal terrane.

Analysis of further characters of the snails themselves can (and should) be used to test the phylogenetic component of this model. The stratigraphic and geographic distribution of the respective clades can be used to test, and develop a time scale for, the historical component. This model predicts that, in paleoenvironments that could support snails of both clades, the home clade will appear stratigraphically below the first appearance of the dispersing clade.

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Appendix

Locality register of figured and referred specimens.

UCM locality number	Location	USGS 7½ min. quadrangle map
83235	260 m W, 260 m N of SW corner, sec. 28, T. 31 N, R. 70 W	Dilts Ranch, WY (1949)
87063	380 m E, 1070 m S of NW corner, sec. 27, T. 31 N, R. 70 W	Orin, WY (1949)
90004	60 m W, 500 m N of SE corner, sec. 28, T. 31 N, R. 70 W	Cedar Hill, WY (1949)
90005	280 m W, 1300 m S of NE corner, sec. 29, T. 31 N, R. 70 W	Irvine, WY (1949)

New Occurrences of the Malleid Bivalve *Nayadina (Exputens)* from the Eocene of Jamaica, Mexico, and Washington

by

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Abstract. New collecting extends the geographic range of two of the three known species of the warm-water, Eocene malleid bivalve *Nayadina (Exputens)*. *Nayadina (E.) batequensis* Squires, 1990, formerly known only from north-central Baja California Sur, Mexico, is now also known from north-western Jamaica and southern Baja California Sur, Mexico. *Nayadina (E.) llajasensis* (Clark, 1934), formerly recognized from southern California to central Oregon is now also known from northwestern Washington.

INTRODUCTION

Nayadina (Exputens) is a warm-water malleid bivalve with Old World Tethyan affinities (PALMER, 1967; GIVENS, 1989). Three species are known: *N. (E.) batequensis* Squires, 1990, from the lower Eocene part of the Bateque Formation, Baja California Sur, Mexico; *N. (E.) llajasensis* (Clark, 1934) from middle lower to lower middle Eocene deposits in southern and central California and central western Oregon; and *N. (E.) ocalensis* (MacNeil, 1934) from upper Eocene deposits in Florida, Georgia, and North Carolina. These species are reviewed and compared in SQUIRES (1990). New collecting has revealed additional occurrences of *N. (E.) batequensis* from Jamaica and Baja California Sur, Mexico, and *N. (E.) llajasensis* from northwestern Washington. It is the purpose of this present study to report on these new occurrences.

Abbreviations used for catalog and/or locality numbers are: CSUN, California State University, Northridge; IGM, Instituto de Geología, Universidad Nacional Autónoma de México; LACMIP, Los Angeles County Museum of Natural History, Invertebrate Paleontology Section; UF, University of Florida, Gainesville.

NEW OCCURRENCES OF *NAYADINA (EXPUTENS) BATEQUENSIS*

The author obtained four specimens of *Nayadina (E.) batequensis* from limestones in the Chapelton Formation in

northwestern Jamaica. LEWIS & DRAPER (1990) assigned this formation to the lower to middle Eocene. Three of the specimens are from locality UF XJ012 near Montego Bay, and one specimen is from locality UF XJ018 near Christiana. Two of these specimens are illustrated (Figures 1–3). Specimen UF 37089 (Figure 3) is larger than those previously known for *N. (E.) batequensis*. Additional collecting from the Bateque Formation, Baja California Sur, Mexico (SQUIRES & DEMETRION, in press), however, has yielded comparable large-sized specimens (Figure 4).

The author obtained three early adult specimens of *Nayadina (E.) batequensis* from sandstones in the upper part of the Tepetate Formation about 75 km north of La Paz in southern Baja California Sur, Mexico. SQUIRES & DEMETRION (1991) showed that these sandstones are coeval with the lower Eocene (“Capay Stage”) part of the Bateque Formation that is about 200 km to the north in north-central Baja California Sur. One of the Tepetate Formation specimens is from locality CSUN 1491, and two other specimens are from locality CSUN 1522. One of the specimens from locality CSUN 1522 is illustrated in Figures 5 and 6.

Nayadina (Exputens) batequensis is the earliest species of *Exputens* and can now be shown to have ranged more easterly than the other species of *Exputens*. The presence of this species in Jamaica and Baja California Sur strongly suggests that either the subgenus emigrated from the Old World into the North America region via the circum-equatorial current that flowed from east to west during



Explanation of Figures 1 to 10

Figures 1–6. *Nayadina (Exputens) batequensis* Squires, 1990. Figures 1–3: Chapelton Formation, Jamaica. Figures 1, 2: hypotype, UF 37088, locality UF XJ012, $\times 2.2$; Figure 1, left valve; Figure 2, dorsum. Figure 3: hypotype, UF 37089, locality UF XJ018, left valve $\times 1.1$. Figure 4: hypotype, IGM 5924, locality CSUN 1470, Bateque Formation, Baja California Sur, Mexico, left valve, $\times 1.1$. Figures 5, 6: hypotype, IGM 5925, locality CSUN 1522, Tepetate Formation, Baja California Sur, Mexico, right valve, $\times 1.8$; Figure 5, dorsum; Figure 6, exterior.

Figures 7–10. *Nayadina (Exputens) llajasensis* (Clark, 1934). Figure 7: hypotype, LACMIP 11525, locality CSUN 1516, from reworked clast of Crescent Formation in the Aldwell Formation, Pulali Point, Washington, right valve, $\times 1.7$. Figures 8–10: locality CSUN 1502, Crescent Formation near Quilcene, Washington; Figure 8, hypotype, LACMIP 11478, right valve, $\times 1.3$. Figures 9–10: hypotype, LACMIP 11489, left valve, $\times 2.1$; Figure 9, dorsum; Figure 10, interior.

the early Eocene or that the subgenus originated in the Jamaica area.

NEW OCCURRENCES OF *NAYADINA (EXPUTENS) LLAJASENSIS*

The author obtained ten specimens of *Nayadina (E.) llajasensis* from Eocene rocks about 45 km west of Seattle, Washington. Six specimens are from reworked sedimentary clasts in the lower part of the middle Eocene Aldwell (?) Formation at locality CSUN 1516 at Pulali Point. Some of the reworked clasts consist of very distinctive whitish-colored, calcareous, medium-grained sandstone most likely derived from the underlying lower Eocene upper part of the Crescent Formation (SQUIRES *et al.*, in press). One of the *N. (E.) llajasensis* specimens is illustrated in Figure 7.

Four other specimens of *Nayadina (E.) llajasensis* are from the upper Crescent Formation at locality CSUN 1502, about 5 km north of Pulali Point. At CSUN locality 1502, the specimens were found in boulder-sized rocks that are not in place but are in a modern landslide block at the base of a steep cliff mapped by HAMLIN (1962) as

Crescent Formation basalt. He did not mention any sedimentary rocks interbedded with the Crescent Formation in this area, but sedimentary interbeds are present (J. L. Goedert, personal communication). Brachiopods are very abundant at locality CSUN 1502, with numerous specimens of *Hemithiris reagani* Hertlein & Grant, 1944, and common specimens of *Terebratulina unguicula weaveri* Hertlein & Grant, 1944. There are also a few specimens of a calcareous? sponge, a single specimen of a new anomiid bivalve, and a single large specimen of *Ostrea* sp. All the associated macrofauna is also present in the upper Crescent Formation at Pulali Point (SQUIRES *et al.*, in press). Additional evidence from the *N. (E.) llajasensis* specimens at CSUN locality 1502 are most likely from the upper Crescent Formation is that the specimens are in a distinctive whitish-colored, calcareous, medium-grained sandstone identical in lithology to some reworked clasts in the basal part of the Aldwell(?) Formation found by SQUIRES *et al.* (in press) at Pulali Point at locality CSUN 1516. Two of the *N. (E.) llajasensis* specimens from CSUN locality 1502 are illustrated (Figures 8–10).

Localities CSUN 1502 and 1516 in northwestern Washington are the northernmost occurrences of any species of

Nayadina (Exputens) and show how extensive warm-water conditions were along the Pacific coast of North America during early to middle Eocene time. Previously, the northernmost occurrence of *Nayadina (Exputens)* was central western Oregon. BALDWIN (1955) reported *Exputens alexi* (Clark, 1934) from the lower Eocene Siletz River Volcanic Series in central western Oregon. SQUIRES (1990) showed that *Exputens alexi* is conspecific with *N. (E.) llajasensis*.

ACKNOWLEDGMENTS

Roger W. Portell (Florida Natural History Museum) informed the author about the Jamaican specimens that he and others collected. He also provided for the loan of the specimens. M. C. Perrilliat (Instituto de Geología, Universidad Nacional Autónoma de México) arranged for permission for paleontologic collecting in Baja California Sur. She also provided the type-specimen numbers. Robert A. Demetron helped in collecting the Baja specimens. James L. Goedert informed the author about the Washington specimens that he and Keith L. Kaler collected. The manuscript was reviewed by E. J. Moore, Oregon State University, Corvallis, and by an anonymous reviewer.

LOCALITIES CITED

CSUN 1471. Near middle of canyon wall along W side of Arroyo San Juan de Abajo, about 80 m elevation, about 0.75 km W of dirt road from San José de Gracia to El Datilon, at 112°44'W and 26°29.5'N, Mexican government 1:50,000 topographic quadrangle map of Punta Santo Domingo (number G12A47), Baja California Sur, Mexico, 1982. Bateque Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: R. L. Squires and R. A. Demetron, April 1990.

CSUN 1491. In a small quarry on S side of Mexico Highway 1, at 74.5 km N of La Paz, coordinates 9.5 and 71.5 of Mexican government 1:50,000 topographic quadrangle map of El Conejo (number G12D81), Baja California Sur, Mexico, 1983. Tepetate Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: R. L. Squires and R. A. Demetron, June 1991.

CSUN 1502. From boulder-sized rocks not in place but in a modern landslide block, 2 km S of Quilcene on W shore of Quilcene Bay just S of latitude 47°47'30", NE¼, section 36, T27N, R2W, Quilcene quadrangle (7.5 minute), 1953, Jefferson County, northwestern Washington. Upper Crescent Formation. Age: Early Eocene (near the boundary between the "Capay Stage" and the "Domengine Stage"). Collectors: J. L. Goedert and K. Kaler, April 1990. (Note: this locality is probably the same as locality University of Washington 353 described by WEAVER (1943:602)).

CSUN 1516. About 20 m above the base of the Aldwell(?) Formation, 1380 m N of tip of Pulali Point, in beach cliff along W shore of Dabob Bay, section 18, T26N,

R1W, Seabeck quadrangle (7.5 minute), 1953, photo-revised 1968, Jefferson County, northwestern Washington. Aldwell(?) Formation. Age: Middle Eocene (Narizian Stage). Collector: J. L. Goedert, June 1990.

CSUN 1522. In a small arroyo about 0.5 km N of Mexico Highway 1, at 75 km N of La Paz, coordinates 9 and 72 of Mexican government 1:50,000 topographic quadrangle map of El Conejo (number G12D81), Baja California Sur, Mexico, 1983. Tepetate Formation. Age: Middle early Eocene ("Capay Stage"). Collector: R. A. Demetron, July 1991.

UF XJ012. Small exposure on W side of road, 5 km S of Johns Hall Quarry, Spring Mount, St. James Parish, Jamaica. Chapelton Formation. Age: Middle Eocene. Collectors: Portell, Bryan, Heller, and Frederick, May 1990.

UF XJ018. Along stream between Pump Station and Wait-A-Bit Cave at Wait-A-Bit, Trelawny Parish, Jamaica. Stettin Member of Chapelton Formation. Age: Early Eocene. Collectors: Portell, Bryan, Heller, and Frederick, May 1990.

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An Eastern Pacific *Mercenaria* and Notes on Other Chionine Genera (Bivalvia: Veneridae)

by

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Abstract. *Chione* (*Lirophora*) *kellettii*, an east Pacific species, is reclassified under *Mercenaria*. Shells of *Mercenaria* are large, with prominent nymphs that are often rugosely sculpted, and with subdued, mostly commarginal sculpture. The prominent rugose nymph, as well as affinities in sculpture, size, and shape, ally *M. kellettii* more closely to *Mercenaria*, while simultaneously demonstrating the transition between *Mercenaria* and the taxa *Anomalocardia* s.s., *Lirophora*, and *Ilioichione*. This transition supports subsuming *Lirophora* and *Ilioichione* under *Anomalocardia* s.s. Additional data, both anatomical and biomolecular, support the reclassification of *Anomalocardia* s.s. and *Mercenaria* as subgenera under the senior taxon, *Chione*.

INTRODUCTION

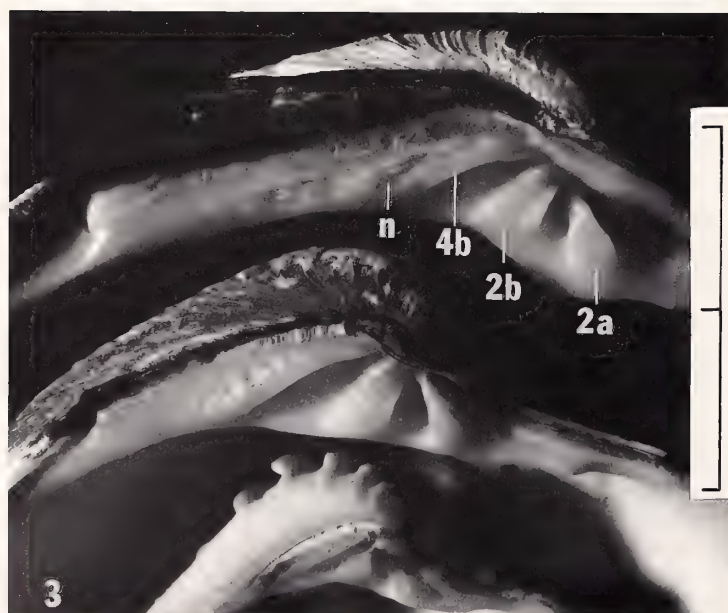
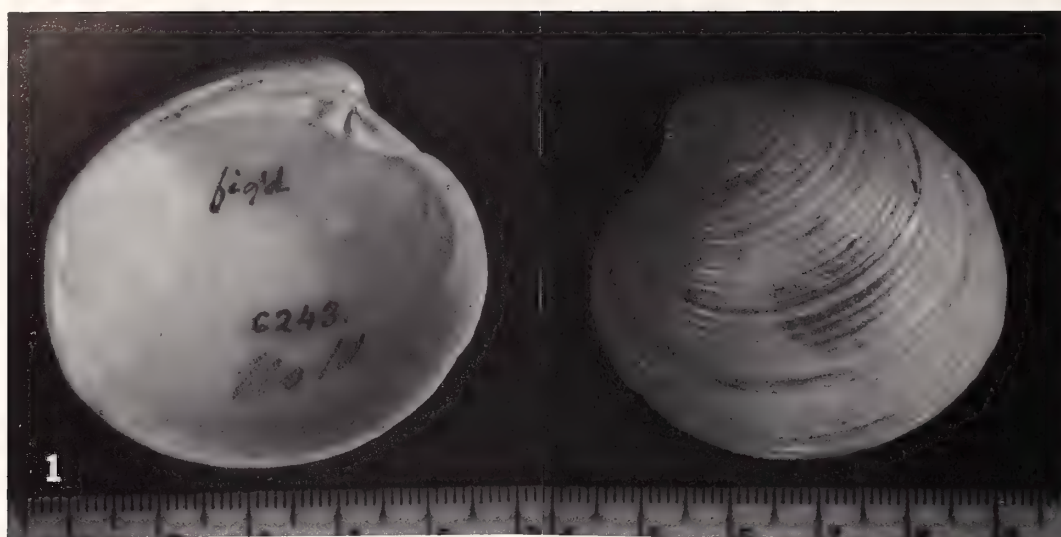
Mercenaria Schumacher, 1817 (Veneridae: Chioninae) is distinguished from other chionine genera primarily in having subdued commarginal sculpture and a prominent, often rugosely sculpted nymph, located posterior to the cardinals. The left posterior cardinal tooth (4b), characteristically a long narrow ridge, is sometimes barely noticeable before the rugose nymph.

Whereas two Atlantic species (*Mercenaria mercenaria* Linnaeus, 1758, and *M. campechiensis* Gmelin, 1791) and one western Pacific species (*M. stimpsoni* Gould, 1861) are recognized, identifying an eastern Pacific *Mercenaria* has been elusive. Living *Mercenaria* observed along the northwest coast of North America were named *M. kennicottii* Dall, 1871, but were later recognized as human introductions of the Atlantic *M. mercenaria* (HANNA, 1966; MORRIS *et al.*, 1980); the type of *M. kennicottii*, U.S. National Museum (USNM) 75017, appears to be a specimen of *M. campechiensis*. The existence of the west tropical American species *Mercenaria apodema* (Dall, 1902) is dubious. The extremely worn condition of the single type valve, USNM 6243 (Figure 1), precludes precise identification; the remains of the cardinal teeth are worn flat and devoid of details such as bifidity. OLSSON (1961) speculates that it is a ballast shell from the Caribbean. It lacks a rugose nymph and, in general, its features more closely resemble some species of *Protothaca* Dall, 1902. The only other reported collection of *M. apodema* was a pair of dead valves that resemble *M. campechiensis*, leading KEEN (1971) to conclude that the existence of a Panamic *Mercenaria*

could not as yet be positively proved. Here, I show that *Venus kellettii* Hinds, 1845, classified under *Chione* (*Lirophora*) by KEEN (1971), is a tropical eastern Pacific *Mercenaria*, and discuss how this genus is related to subgenera of *Chione* and *Anomalocardia*.

MATERIALS AND METHODS

Valves of *Mercenaria mercenaria*, *M. campechiensis*, *M. stimpsoni*, *Chione* (*Lirophora*) *kellettii*, and *C. (L.) latilirata* (Conrad, 1841) were examined from the collections at the Museum of Paleontology, University of California at Berkeley, and the California Academy of Sciences (CAS), using a dissecting scope and a 10× magnifying glass. I also examined the nymphs of species representing the other extant genera and subgenera of *Chione* and *Anomalocardia*: of *Chione* s.s.—*C. cancellata* (Linnaeus, 1767), *C. californiensis* (Broderip, 1835), *C. compta* (Broderip, 1835), *C. intapurpurea* (Conrad, 1849), *C. subimbricata* (Sowerby, 1835), *C. tumens* Verrill, 1870, and *C. undatella* (Sowerby, 1835); of *Chione* (*Austrovenus*)—*C. stutchburii* (Gray, in Wood, 1828); of *Chione* (*Chionista*)—*C. fluctifraga* (Sowerby, 1853) and *C. cortezi* (Carpenter, 1864); of *Chione* (*Chionopsis*)—*C. amathusia* (Philippi, 1844), *C. gnidia* (Broderip & Sowerby, 1829), *C. ornatissima* (Broderip, 1835), and *C. pulicaria* (Broderip, 1835); of *Chione* (*Ilioichione*)—*C. subrugosa* (Wood, 1828); of *Chione* (*Lirophora*)—*C. clenchi* Pulley, 1952, *C. mariae* (Orbigny, 1846), and *C. paphia* (Linnaeus, 1767); of *Anomalocardia* s.s.—*A. brasiliensis* (Gmelin, 1791) and *A. cuneimeris* (Conrad, 1846); of *Anomalocardia* (*Anomalodiscus*)—*A. squamosa*



(Linnaeus, 1758); of *Anomalocardia* (*Cryptonomella*)—*A. producta* (Kuroda & Habe, in Kuroda, 1951).

OBSERVATIONS

SCHUMACHER (1817) defined the shells of *Mercenaria* as triangular, heart-shaped and somewhat obese, with the 2a, 2b, 1, and 3b cardinals bifid, and with a prominent, rugose nymph. In addition, the sculpture of the valves consists of closely spaced, sharp, commarginal threads that sometimes become obsolete medially, forming smooth areas; fine, faint radials are often partly evident. The prominent nymph is probably the most consistent trait of this genus. The mature shells are relatively large for chionines (7–15 cm).

The nymph of *Mercenaria kellettii* is clearly more similar to *Mercenaria* (Figure 3) than *Chione* (*Lirophora*): the nymph is prominent, roughly twice the length of the posterior cardinal (4b), with a wide, rugosely sculpted area. The nymph of *C. latilirata*, by contrast, is not prominent, limited to the length of the posterior cardinal, and narrow, with the rugose area barely noticeable between the cardinal and the ligament.

The rugose area of the *Mercenaria* nymph varies from being wide and large in most *M. mercenaria* to thinner and smaller (some specimens of *M. campechiensis*). In *M. stimpsoni*, the nymph is prominent but smooth, with the rugose area restricted to a narrow, barely noticeable strip on the posterior flank of the 4b. Within this range, the nymph of *M. kellettii* is intermediate, and quite similar to some *M. campechiensis*. The rugose nymph of *M. kellettii* is not mentioned in its original description (HINDS, 1845) nor in its descriptions by subsequent workers (e.g., KEEN, 1971; OLSSON, 1961), although a rugose nymph is evident in the illustration of the hinge by OLSSON (1961:pl. 41, fig. 5).

The sculpture of the type species of *Mercenaria*, *M. mercenaria*, consists of fine concentric threads, which can become obsolete medially to form smooth areas while becoming slightly lamellar laterally. Some threads can also develop into low, thin, continuous, moderately spaced, concentric lamellae that are evident on juveniles and some adults; fine, faint radials are sometimes evident on some part of the valve. Except for some of the lateral lamellae that are developed into pronounced flanges, the sculpture of *M. kellettii* fits that of *M. mercenaria*; fine concentric threads become obsolete medially forming smooth areas, sometimes over most of the shell. Fine, faint radials are

sometimes evident on some part of the valve. *Mercenaria kellettii* differs from other species of *Chione* (*Lirophora*), which have strong sculpture over most of the valves (Figure 2), although the sculpture of *M. kellettii* illustrates the similarities linking *Mercenaria* to *Chione* (*Lirophora*): well spaced intervals of the *M. mercenaria* valve are demarcated by sulci that are slightly deeper than those separating other concentric threads. In *M. kellettii*, these sulci demarcate areas that terminate in pronounced lateral flanges, and in *Chione* (*Lirophora*), these areas are pronounced, thickened lirae. In *M. kellettii*, the bounded areas sometimes appear slightly swollen, reminiscent of the thickened lirae in *Lirophora*.

In other respects, the characters of *Mercenaria kellettii* are well within the character range of *Mercenaria*, and include a similar lunule, escutcheon, pallial sinus, cardinals, and hinge plate. The differences from other *Mercenaria* appear slight. The profile of *M. kellettii* is slightly more elongate than that of most *Mercenaria*; the average size (7 cm) is intermediate between *Chione* (*Lirophora*) (3–4 cm) and other *Mercenaria* (10 cm). Unlike other species of *Mercenaria*, *M. kellettii* appears to be almost exclusively offshore (50 m or more), and occurs from the Gulf of California to northern Peru (KEEN, 1971).

The condition of the nymph appears to be a consistent character within the chionine genera and subgenera examined. Besides *Mercenaria*, only the type subgenus of *Anomalocardia* and the *Chione* subgenera *Lirophora* and *Ilioichione* have rugose nymphs. In all four taxa, radial sculpture is usually faint, sparse, or absent. Both *Ilioichione* and *Anomalocardia* have, like *Lirophora*, thick, well spaced concentric lirae, which become less prominent in some species or specimens. Between the attenuated posterior so distinctive of *Anomalocardia* and the slightly angular posterior of most *Mercenaria*, specimens of *M. kellettii* (Figure 2) and species of *Lirophora* and *Ilioichione* form a conchological transition in size, shape, and sculpture. *Ilioichione* has been classified as *Anomalocardia* by some workers (e.g., HERTLEIN & STRONG, 1948).

Fossil evidence indicates that *Chione* evolved from *Mercenaria* (STENZEL, 1955); JONES (1979) suggests that the conchological evolution resulted from neoteny. Unlike *Mercenaria mercenaria*, both the west Pacific *C. (Austrovenus) stutchburii* and the west Atlantic *C. (Chione) cancellata* (type species of the genus *Chione*) have well spaced commarginal cords or lamellae overlying prominent radial ribs.

Explanation of Figures 1 to 3

Figure 1. The interior (left) and exterior (right) valves of the holotype of *Mercenaria apodema*, USNM 6243.

Figure 2. The exteriors of *Mercenaria mercenaria*, CAS 2947, top, *Chione* (*Lirophora*) *kellettii*, CAS 17736, middle, left and right, and *Chione* (*Lirophora*) *latilirata*, CAS 47841, bottom.

Figure 3. Left hinge plates of *Mercenaria mercenaria* (CAS 2947), top, with 2a, 2b, and 4b cardinal teeth and nymph (n) indicated; *Chione* (*Lirophora*) *kellettii* (CAS 17736), middle, and *Chione* (*Lirophora*) *latilirata* (CAS 47841), bottom; 2 cm scale bar, right.

While *C. stutchburii* is much more similar to *C. cancellata* than to *M. mercenaria* in valve sculpture, *C. cancellata* and *M. mercenaria* are much more similar in anatomy (JONES, 1979). Additionally, *C. (Liophora) paphia* is slightly more similar to *C. cancellata* than to *M. mercenaria* in anatomy (JONES, 1979), although one of the few differences between *C. paphia* and *M. mercenaria*, size of the palp rugae, is related probably to differences in the turbidity of their environment (JONES, 1979). *Anomalocardia* was not included in this comparison. Biomolecular evidence (HARTE, in press) indicates that *Anomalocardia s.s.*, while closely related to both *M. mercenaria* and *C. cancellata*, is more closely related to *M. mercenaria*.

CONCLUSIONS

The sculpture and rugose nymph of *Chione (Liophora) kellettii* (Hinds, 1845) are diagnostic of the genus *Mercenaria*, not *Chione (Liophora)*. Other characters of this species fit well within *Mercenaria*, and I propose that the species be reclassified as *Mercenaria kellettii* (Hinds, 1845). The definition of *Mercenaria* should be modified to include those species with a prominent nymph and, specifically, those in which the nymph or part of the 4b cardinal is rugosely sculpted. A rugose nymph and predominantly concentric sculpture, as well as transitions in sculpture and profile, ally some *Chione* subgenera (*Liophora* and *Ilio-chione*) and *Anomalocardia s.s.* to *Mercenaria*. The transition from *Liophora* and *Ilio-chione* to *Anomalocardia* is relatively slight and continuous, and this might be more accurately indicated by subsuming them both under *Anomalocardia s.s.* A more accurate taxonomic classification of *Anomalocardia s.s.*, *Mercenaria*, and *Chione s.s.* might be one in which all three taxa are subgeneric members of the senior taxon, *Chione*. Further studies, both anatomical and biomolecular, are needed to understand how the remaining American subgenera of *Chione* would be classified within this scheme.

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On the Validity, Authorship, and Publication Date of the Specific Name *Ancistrocheirus lesueurii* (Cephalopoda: Ancistrocheiridae)

by

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Abstract. Analysis of the “*Histoire naturelle générale et particulière des Céphalopodes Acétabulifères vivants et fossiles*” by Férussac & d’Orbigny (1834–1848) indicates that *Ancistrocheirus lesueurii* (d’Orbigny, 1842) is the valid name to be applied to the only known species of the genus *Ancistrocheirus*.

INTRODUCTION

Traditionally, two nominal species have been attributed to the family Ancistrocheiridae, formerly subfamily Ancistrocheirinae of the family Enoploteuthidae (CLARKE, 1988): *Ancistrocheirus lesueurii* (d’Orbigny, 1839) and *Thelidioteuthis alessandrinii* (Verany, 1851) (e.g., CLARKE, 1966). (The spelling *lesueurii* and *alessandrinii*, with a double *i* ending, is herein adhered to, in compliance with the *International Code of Zoological Nomenclature* [ICZN, 1985:Art. 33d].) Through a study on juvenile and subadult stages, NESIS (1978) demonstrated that *Thelidioteuthis* was a synonym of *Ancistrocheirus*. At present, it is generally agreed that the two names were given to two different phases of the life cycle of a single species, *A. lesueurii* for the adult and *T. alessandrinii* for an early juvenile stage. Thus, in accordance with the principle of priority (ICZN, 1985: Art. 23), *A. lesueurii* is the binomen currently used (e.g., OKUTANI, 1976; ROPER *et al.*, 1984; ROPER *et al.*, 1985; CLARKE, 1986).

The 1987 English translation of Nesis’ *Cephalopods of the World*—the original work in Russian was published in 1982—raised the issue of the correct specific name to be used. According to NESIS (1978:448; 1987:181) there are two nominal species, i.e., “*Ancistrocheirus alessandrinii* (Vérany, 1851)” and “*Ancistrocheirus lesueuri* Férussac et d’Orbigny, 1839,” the latter of which he believes is a doubtful species. However, NESIS (1987:171) also states that *Ancistrocheirus lesueurii* is the type species, so some confusion is present. In another work, NESIS (1984) lists only *Ancistrocheirus alessandrinii*.

The purposes of this paper are, first, to establish the valid specific name to be applied to the ancistrocheirid

squid under discussion and, second, to determine its authorship and publication date.

SPECIFIC NAME

According to NESIS (1987), the difference between the nominal species *Ancistrocheirus lesueurii* and *Ancistrocheirus alessandrinii* involves the distribution of the large photophores on the ventral side of the mantle. In *A. alessandrinii* they are “arranged in alternating groups of fours and twos, not forming unpaired longitudinal row and not extending to tail” (NESIS, 1987:180–181); in *A. lesueurii* they form “(in addition to twos and fours) unpaired median longitudinal row and extend to tail” (NESIS, 1987:181). The total number of photophores in both species is 22. The general distribution of photophores of *A. alessandrinii sensu* NESIS (1987) is in agreement with that given by OKUTANI (1976) and ROPER *et al.* (1984, 1985) for *A. lesueurii*, whereas the photophore arrangement of *A. lesueurii sensu* NESIS (1987:181) is “4+2+3+3+2+2+3+1+1+1.” Such a photophore distribution is clearly taken from FÉRUSAC & D’ORBIGNY (1834–1848: atlas, plate 14 ONYCHOTEUTHE [*Onychoteuthis*], fig. 4) (see Figure 3, herein). Indeed there is a discrepancy between the number of photophores (22) depicted in this figure and the description given by FÉRUSAC & D’ORBIGNY (1834–1848:339–340): “le corps est lisse en dessus, marqué en dessous de tubercules saillants [= photophores] au nombre de 21, très régulièrement disposés.” Such a discrepancy may simply represent a typographical error. Otherwise it can be attributed to the fact that d’Orbigny did not attach a primary taxonomic importance to that character, or did not make a close enough check of the number and position

of photophores on the specimen or in the figure that depicts the specimen itself. In regard to this, it is noteworthy that the specimen described in FÉRUSAC & D'ORBIGNY (1834–1848:atlas, plate 14 of the genus *Onychoteuthis*; text, 339–340) was taken from a dolphin stomach (LU *et al.*, in press), so that the predator digestion processes might have wholly or partly destroyed the integument and its annexes, including photophores. The above-mentioned specimen, which represents the holotype of the d'Orbigny species and is kept at the Muséum National d'Histoire Naturelle of Paris, catalogue No. MNHN 2-14-614, was also examined by the author. Unfortunately, the specimen is in bad condition. The skin is lacerated and largely missing on the ventral surface of the mantle; the “tail” completely lacks the skin. Only a few photophores are present and, possibly, displaced to some extent from their natural position. Apparently, none of them lies on the sagittal line, *i.e.*, in unpaired position. It is not known whether the specimen was already in bad condition when described by d'Orbigny or deteriorated afterwards.

Lastly, NESIS stated (1987:181) that the distribution and habitat of *Ancistrocheirus lesueurii* Férussac & d'Orbigny, 1839, are unknown. Indeed d'Orbigny (*in* FÉRUSAC & D'ORBIGNY, 1834–1848:340) reported the *locus typicus*: “*Hab. Le grand Océan*,” which corresponds to the Indo-Pacific, as shown by internal evidence. GRAY (1849) reported the Indian Ocean as the *locus typicus*.

To sum up, NESIS (1987) doubted the identity of *Ancistrocheirus lesueurii* largely, if not entirely, on the basis of the photophore arrangement depicted by FÉRUSAC & D'ORBIGNY (1834–1848:atlas, plate 14 of the genus *Onychoteuthis*). In fact, the same work (FÉRUSAC & D'ORBIGNY, 1834–1848:339–340) presented a fairly long and sufficiently discriminating description of *A. lesueurii*. Therefore, the nominal taxa “*Ancistrocheirus alessandrinii* (Vérany, 1851)” and “*Ancistrocheirus lesueuri* Férussac & d'Orbigny, 1839” accepted by NESIS (1978:448; 1987:181) are herein considered to be synonymous. On the basis of priority (ICZN, 1985:Art. 23), *A. lesueurii* is the valid name.

AUTHORSHIP AND PUBLICATION DATE

Determining the correct authorship and publication date of *Ancistrocheirus lesueurii* is a somewhat more complicated

problem. Usually the species is referred to d'Orbigny, 1839 (*e.g.*, CLARKE, 1966, and subsequent authors).

The specific name *lesueurii* appeared for the first time and was repeatedly referred to in *Histoire naturelle générale et particulière des Céphalopodes Acétabulifères vivants et fossiles* by FÉRUSAC & D'ORBIGNY (1834–1848). WINCKWORTH (1942) elucidated the publication dates of the 21 parts, issued separately, that make up the work. Additional information on the publication dates of the herein discussed taxa is reported by LU *et al.* (in press) and TILLIER & BOUCHER-RODONI (in press).

The chronological order of the appearance of the name *lesueurii* in FÉRUSAC & D'ORBIGNY (1834–1848) is reported below, with related comments.

(1.) “*Onychoteuthis Lesueurii*, d'Orbigny,” 1835, plate 4 of the genus *Onychoteuthis*.

This drawing is by d'Orbigny (“A. d'Orbigny pinx.”), who stated that the plate was printed in 1825 (FÉRUSAC & D'ORBIGNY, 1834–1848:331). According to WINCKWORTH (1942), the heading “*Cryptodibranches*” proved that the plate was part of a group that was printed in the period 1825–1833 and issued in the years 1834–1835. As stated by WINCKWORTH (1942:35) “these plates may then be definitely dated as 1835.” LU *et al.* (in press) and TILLIER & BOUCHER-RODONI (in press) also date the plate as 1835; it was issued in *livraisons* 4–6, March 1835 (TILLIER & BOUCHER-RODONI, in press).

The cephalopod portrayed in the plate under discussion (see Figure 1 herein) is a true *Onychoteuthis* (*cf. banksii*). Later, d'Orbigny himself (*in* FÉRUSAC & D'ORBIGNY, 1834–1848:330–332) listed his *O. lesueurii* of plate 4 among the synonyms of *Onychoteuthis banksii* (Leach, 1817): “en 1826, j'ai imposé à tort le nom de *Onychoteuthis Lesueurii* à un exemplaire [of *O. banksii*] rapporté par M. Lesueur.”

LU *et al.* (in press) remark that “the holotype of this species is also a syntype of *Onykia angulatus* Lesueur, 1821, which was sent by Lesueur to Férussac and appeared in Férussac & d'Orbigny (pl. 4) under the name *Onychoteuthis lesueuri*.” This type specimen is still extant and is kept at the Muséum National d'Histoire Naturelle of Paris: holotype, MNHN 3-1-628, female, ML = 72 mm; MNHN 3-1-643 (gladius, dry) (LU *et al.*, in press).

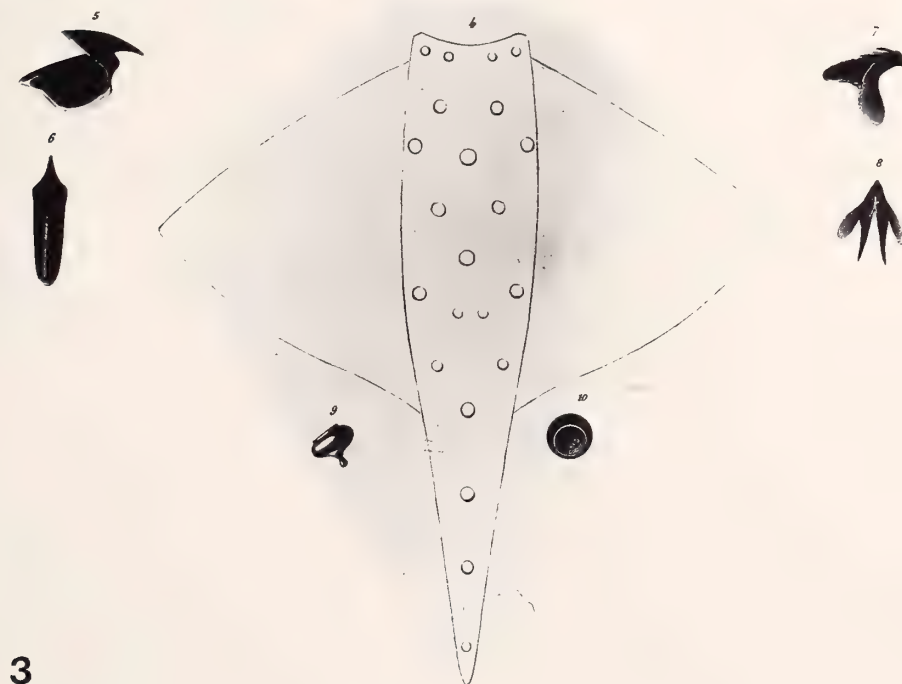
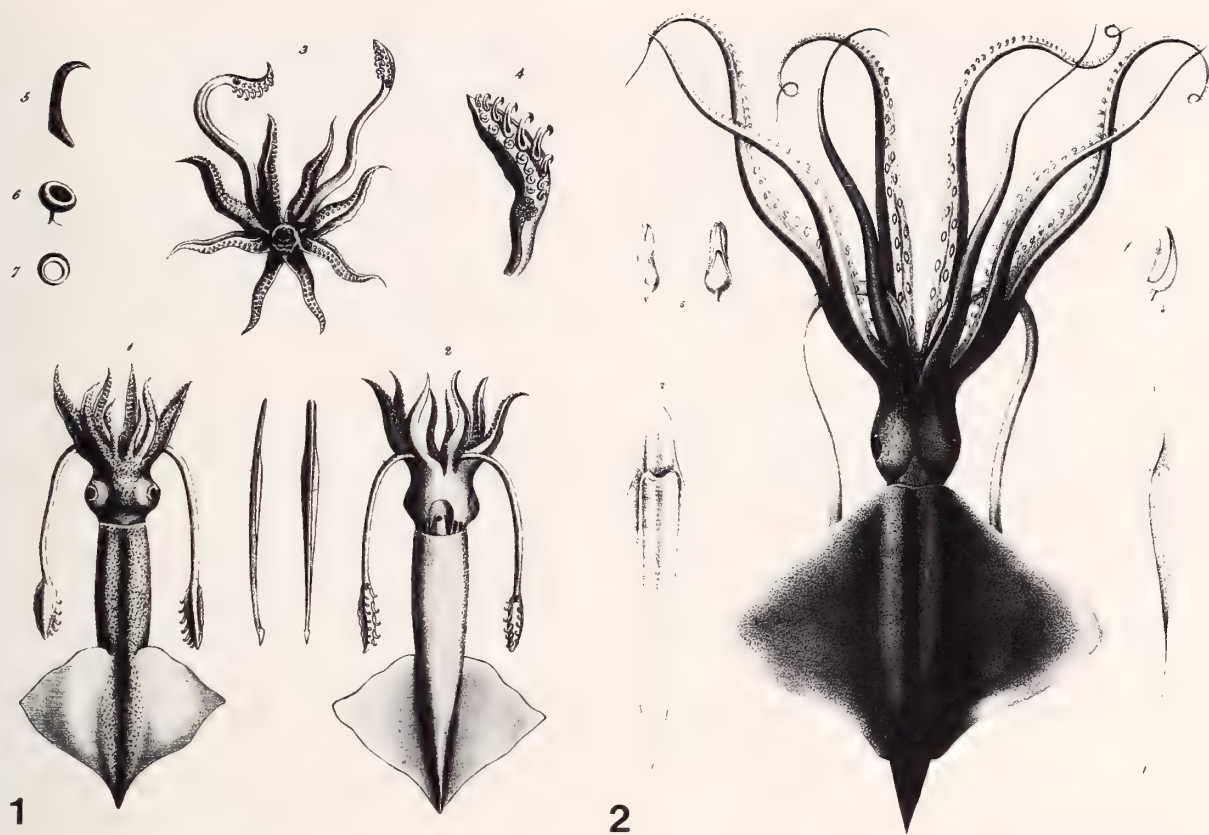
(2.) “*Onychoteuthis Lesueurii*, Férussac,” 1835, plate 11 of the genus *Onychoteuthis*, figs. 1–5.

Explanation of Figures 1 to 3

Figure 1. “*O. Lesueurii*, d'Orbigny”; pl. 4 of the genus *Onychoteuthis*, figs. 1–7; from FÉRUSAC & D'ORBIGNY (1834–1848). The plate represents a specimen of *Onychoteuthis cf. banksii*. Key: 1–2, dorsal and ventral views; 3, oral view of arms and tentacles; 4, tentacle club; 5, hook; 6, sucker; 7, sucker ring; not numbered, gladius.

Figure 2. “*O. Lesueurii*, Férussac”; pl. 11 of the genus *Onychoteuthis*, figs. 1–5; from FÉRUSAC & D'ORBIGNY (1834–1848). The figures represent *Ancistrocheirus lesueurii*. Key (faint in original): 1, dorsal view; 2–3, gladius; 4–5, arm hook.

Figure 3. “*Enoplateuthis Lesueurii*, d'Orbigny”; pl. 14 of the genus *Onychoteuthis*, figs. 4–10; from FÉRUSAC & D'ORBIGNY (1834–1848). The figures represent *Ancistrocheirus lesueurii*. Key: 4, ventral view of mantle; 5–6, upper mandible; 7–8, lower mandible; 9–10, “*tubercule*” [= photophore].



According to d'Orbigny (*in* FÉRUSAC & D'ORBIGNY, 1834–1848:339) this plate was printed in 1835. In addition, it bears Férussac's name, which supports the assumption that it was printed before Férussac's death in 1836. WINCKWORTH (1942) included this plate in a group published in the period 1839–1841. He also reported that the plate might have been issued as early as 1835, in the 11th *livraison* (WINCKWORTH, 1942). In fact, TILLIER & BOUCHER-RODONI (*in press*) show that plate 11 was issued with *livraisons* 10–11, in June 1835.

There is no doubt that the species portrayed is *Ancistrocheirus lesueurii* (Figure 2 herein).

The type specimen of *Onychoteuthis lesueurii* Férussac is no longer extant. At the Muséum National d'Histoire Naturelle of Paris there is a gladius that might belong to the type specimen (Boucher-Rodoni, personal communication).

(3.) "*Enoplateuthis Lesueurii*, d'Orbigny," 1842, plate 14 of the genus *Onychoteuthis*, figs. 4–10.

Despite the fact that d'Orbigny (*in* FÉRUSAC & D'ORBIGNY, 1834–1848:339) dated this plate as 1835, certain details (reported below) show that it was printed at a later date than plate 11 of the same genus. It is, in fact, part of a batch of plates—some of which may be fairly safely dated as 1838–1839—prepared by a single lithographer and a single printing house. The new genus *Enoplateuthis*, which included the species *lesueurii*, was established by d'Orbigny (*in* FÉRUSAC & D'ORBIGNY, 1834–1848: 336–337) after he took up the work again in 1837, following Férussac's death, and completely reviewed the taxonomy. According to WINCKWORTH (1942:36), the plate publication date is "[1839–]1848" and since "in systematic work the dates in brackets should be omitted," the official publication date should be 1848. However the *Enoplateuthis lesueurii* plate is mentioned in another work by D'ORBIGNY (1845), evidence that it was issued well before 1848. In fact, the plate was issued sometime during the years 1839–1842 (*vide* TILLIER & BOUCHER-RODONI, *in press*). There is no clue to ascertain the exact year of publication. Thus, it is herein concluded that the publication date to be used for taxonomic purposes is 1842, in accordance with Art. 21 of the ICZN (1985).

The customarily used date of 1839 is attributable to GRAY (1849), who assigned that publication date to plate 14, without giving any evidence for it. The dates reported by GRAY (1849) are not reliable because of several internal discrepancies. (For instance, GRAY [1849] assigned two different publication dates to plate 11 of the genus *Onychoteuthis* of FÉRUSAC & D'ORBIGNY's atlas (1834–1848); e.g., "*Onychoteuthis leptura* Férussac, Céph. Acét. *Onychoteuthis*, t. 11. f. 6–14. 1839" (GRAY, 1849:47) and "*Onychoteuthis Lesueurii* Féruss. & d'Orb. Céph. Acét. *Onych.* t. 11. f. 1–5, animal, 1835" (GRAY, 1849:49). It appears that GRAY (1849) uncritically reported the dates given by d'Orbigny [*in* FÉRUSAC & D'ORBIGNY, 1834–1848]).

Plate 14 represents the species known today by the name *Ancistrocheirus lesueurii* (Figure 3).

Afterwards, d'Orbigny (*in* FÉRUSAC & D'ORBIGNY, 1834–1848:339–340) also gave a fairly complete description of "*Enoplateuthis Lesueurii*." There is no doubt that the publication date of these text pages is 1848 (WINCKWORTH, 1942; TILLIER & BOUCHER-RODONI, *in press*).

The holotype figured in plate 14 is kept at the Muséum National d'Histoire Naturelle of Paris: MNHN 2-14-614, male, ML = 130 mm; MNHN 2-14-615 (gladius, dry); MNHN 2-14-616 (beaks). It was collected by Dussumier from the stomach of a dolphin, in 1835; locality unknown (LU *et al.*, *in press*).

CONCLUSIONS

From what has been reported above, it can be deduced that:

(a.) *Onychoteuthis Lesueurii* d'Orbigny, 1835 *in* FÉRUSAC & D'ORBIGNY, 1834–1848 (*liv.* 4–6) is an available name (ICZN, 1985:Art. 10a) and is a junior synonym of *Onychoteuthis Banksii* (Leach, 1817).

(b.) *Onychoteuthis Lesueurii* Férussac, 1835 *in* FÉRUSAC & D'ORBIGNY, 1834–1848 (*liv.* 10–11) is a primary junior homonym (ICZN, 1985:Art. 57b) of *Onychoteuthis Lesueurii* d'Orbigny, 1835, and as such is permanently invalid (ICZN, 1985:Art. 52b).

(c.) *Enoplateuthis Lesueurii* d'Orbigny, 1842 *in* FÉRUSAC & D'ORBIGNY, 1834–1848, is the next available published name and must replace the invalid *Onychoteuthis Lesueurii* Férussac, 1835 (ICZN, 1985:Art. 60a). The name was proposed in association with illustrations of the species being named, which constitutes an "indication" (ICZN, 1985:Art. 12a[7]).

The original spelling of the specific name, *Lesueurii*, should begin with a lower case letter (ICZN, 1985:Art. 28) and the double "i" ending should be maintained. The spelling with a single "i," i.e., *lesueuri*, is incorrect (ICZN, 1985:Arts. 32, 33).

In conclusion, and taking into account that the species *Enoplateuthis Lesueurii* was later assigned to the genus *Ancistrocheirus* Gray, 1849, the name to be used is *Ancistrocheirus lesueurii* (d'Orbigny, 1842 *in* FÉRUSAC & D'ORBIGNY, 1834–1848).

ACKNOWLEDGMENTS

I am grateful to Dr. C. F. E. Roper, Dr. M. J. Sweeney, and Prof. T. Okutani, who kindly reviewed an early version of the paper and offered criticism, and to an anonymous reviewer for pertinent comments and suggestions. Thanks are due to Dr. R. Boucher-Rodoni for information and discussion on Férussac and d'Orbigny type specimens and works; she also made the holotype of *Ancistrocheirus lesueurii* available. Lastly, I wish to thank Mme. C. Favarger (Muséum d'Histoire Naturelle of Geneva) who courteously provided the photographs of Férussac and d'Orbigny's plates.

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The Anatomy of *Arion flagellus* Collinge, 1893, Present on the Iberian Peninsula (Gastropoda: Arionidae: Terrestria Nuda)

by

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Abstract. The presence of *Arion flagellus* in Galicia (NW Spain) is reported. The internal and external morphology (including spermatophore) and copulation of Galician specimens are described, and are discussed with reference to English specimens and to the Portuguese Arionidae described in the last century by Morelet, Mabilie, Pollonera, and Simroth.

INTRODUCTION

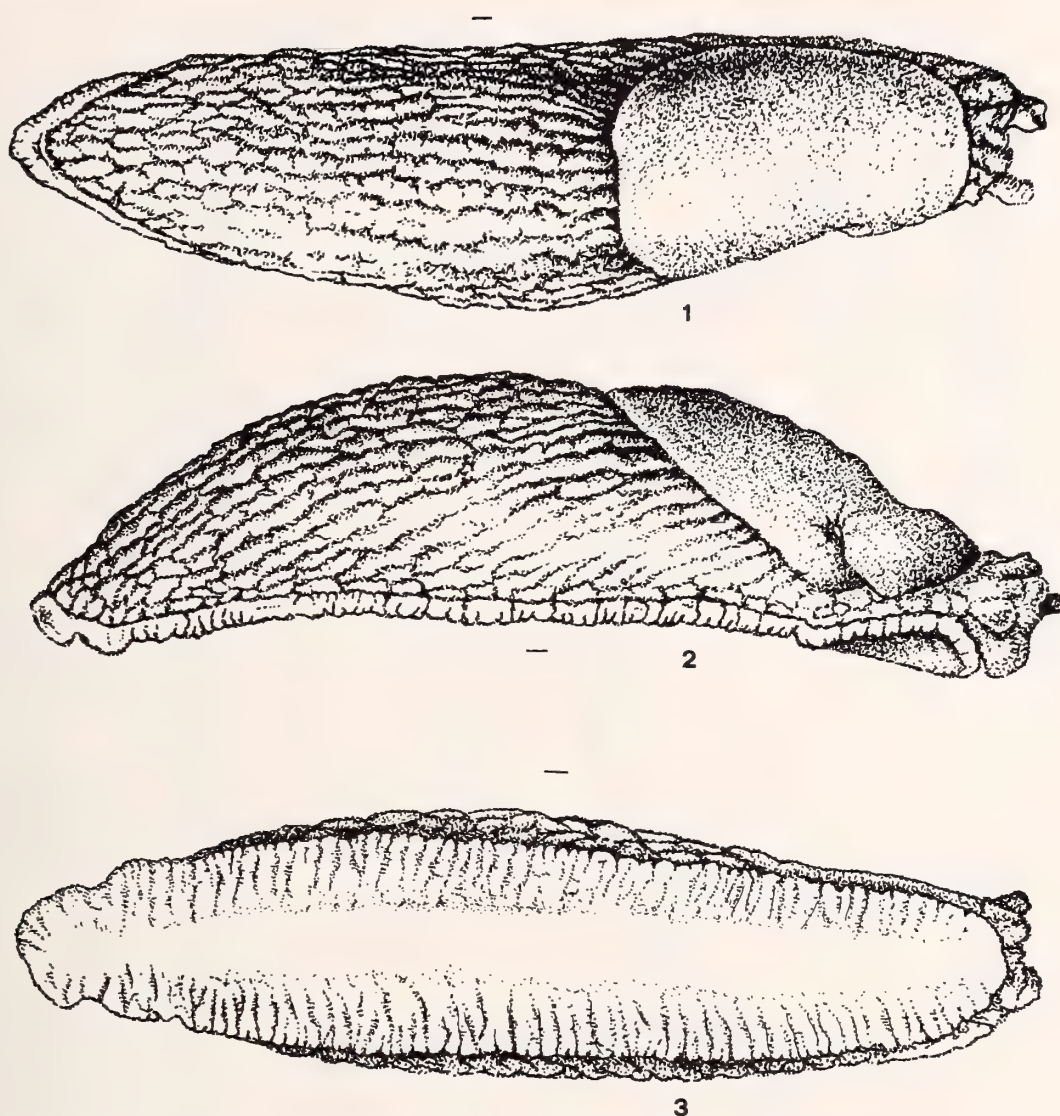
Specific identification of the large Arionidae (the large Arionidae are taken to be those that measure at least 80 mm *in vivo*) of the Iberian Peninsula is difficult if the considered individuals are few in number or incompletely developed. Juveniles may have bands on their mantles and backs that may no longer be present in adults, and body coloring is generally lighter in juveniles than in adults. Many juveniles have a whitish or light gray sole, which in adults, depending on the species, becomes orange, yellowish, black, or light in the center and dark laterally. The genitalia of juveniles are easily distinguished from those of subadults or adults, but those of subadults, adults, and seniles are harder to tell apart, all three sets being completely developed and differing only in the relative proportions of their parts. Identification based on the genital morphology of a small number of specimens is further complicated by the fact that in specimens that have recently copulated (as demonstrated by the presence of the whole spermatophore in the genitalia) the epiphallus is larger in diameter and shorter than in specimens that have a fragmented spermatophore or have not mated.

One structure that can, in principle, give information about the identity of species is the spermatophore. DAVIES (1987) noted that a distinctive form of spermatophore must indicate the reproductive isolation of a good species, and she went on to assert that if each variable species of *Arion* is characterized by the possession of a distinctive, and much less variable, spermatophore, then the organs concerned in the production and exchange of spermatophores must be

of considerable taxonomic importance. Clearly the length of the spermatophore must be of some importance, since long ones will take longer to be exchanged than short ones. The sculpture of the spermatophore, which is produced by the lumen of the epiphallus, may also be significant for transfer. The ligula and copulatory behavior ought to be important too, although DAVIES (1987) pointed out that in stabilizing the pair, and perhaps in stimulating the mating process, the position and movements of the ligula may be more important than its changeable shape and size; upon evagination, in some species the ligula is firmly pressed against that of the mate, in others it is rested on the mate's flanks, and in still others it is used to embrace the mate's tail.

Thus, the identification of species within the Arionidae is not easy, since the sizes and proportions of their organs can vary with both intrinsic factors (developmental stage, cycle phase, *etc.*) and extrinsic factors (degree of relaxation upon death, preservation, manipulation, *etc.*). SIMROTH (1889), recognizing the problem, wrote that the dividing lines between the species of the genus *Arion* are less clear than those between the Limacidae, which is why new species are so easily created. He also felt that what would best enable us to judge what ought to be included under the same name is knowledge of the fauna as a whole, starting from postembryonic development and biology; for Simroth, this investigation would have to take place on the west coast of Europe, the center of the creation of the Arionidae.

The situation outlined above, together with methodological advances in the study and description of new taxa,



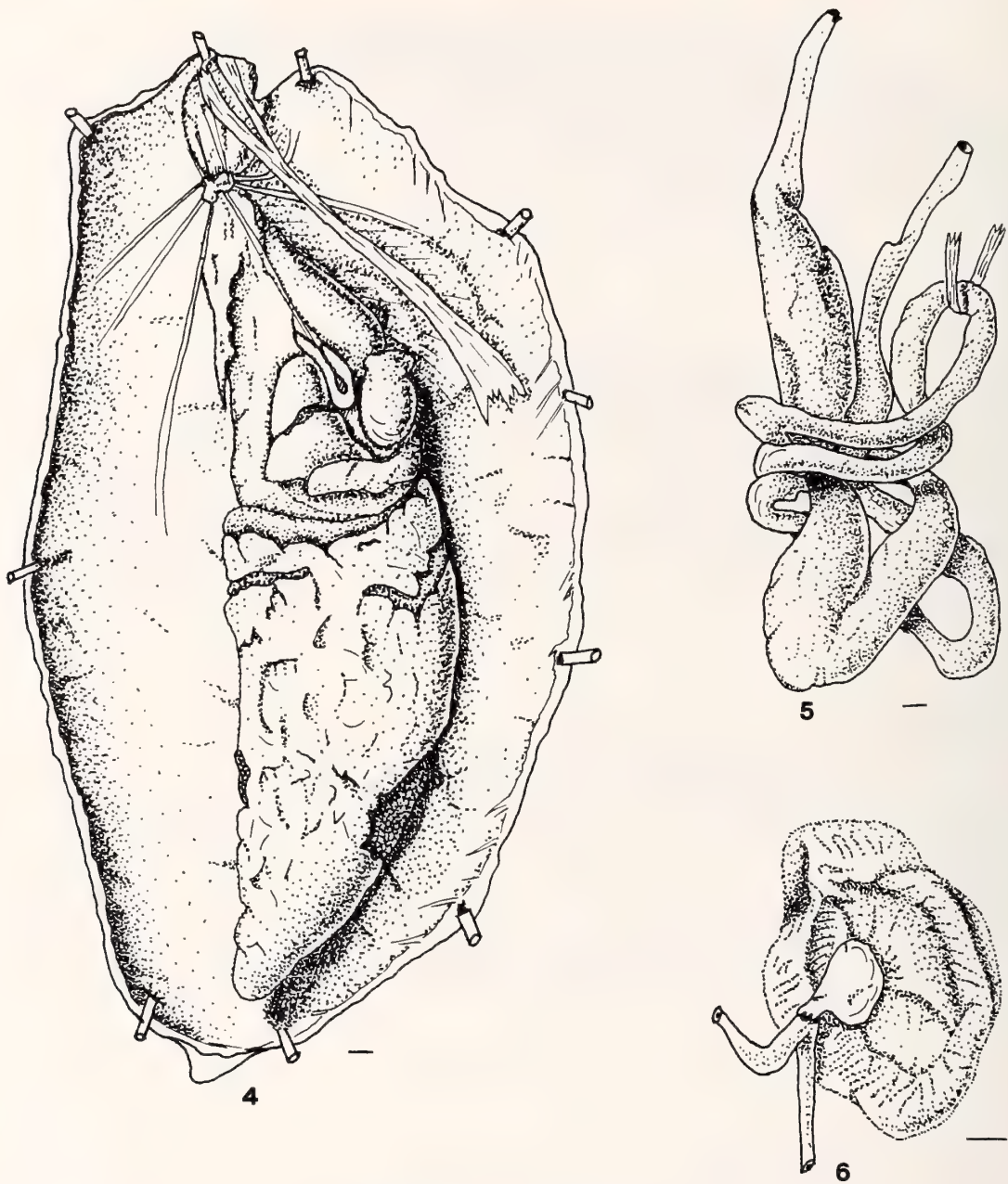
Explanation of Figures 1 to 3

Figures 1–3. *Arion flagellus*, Sierra del Gistral (Lugo). Dorsal, lateral, and ventral views. Scale 1 mm.

make it desirable to re-examine the types, and preferably also the topotypes, of all the species described in the last century on the basis of few and often incompletely developed specimens. This re-examination should be supported by the study of whole populations in various biotopes and in all seasons in order to determine the spatial and temporal variability of the species. Only in this way can the lines dividing species be firmly established.

Arion flagellus was described by COLLINGE (1893) from Ireland. The large Portuguese *Arion* species were studied in the last century by MORELET (1845), MABILLE (1868), POLLONERA (1887, 1889, 1890), and SIMROTH (1886, 1891). Morelet described, solely on the basis of external morphology, a series of new species (*A. sulcatus*, *A. timidus*, and *A. fuliginus*) and re-described several existing species.

Mabille included Morelet's new species in his genus *Baudonia*, and created *A. lusitanicus* with part of *A. rufus sensu* Morelet, and *A. pascalianus* with *A. fuscatus sensu* Morelet. All of Morelet's and Mabille's species were accepted by Pollonera, who also described two new species (*A. dasilvae* and *A. nobrei*). SIMROTH (1886) created *A. hispanicus*, but later recognized only *A. ater* and *A. lusitanicus* as good species, treating *A. hispanicus* as a synonym for the latter. NOBRE (1941) considered all large Portuguese *Arion* to be *A. ater*. SEIXAS (1976), however, reported finding *A. ater*, *A. lusitanicus* and *A. subfuscus*, and CASTILLEJO & RODRÍGUEZ (submitted) recently recognized *A. ater*, *A. nobrei*, *A. lusitanicus*, *A. fuliginus*, and *A. intermedius* in a revision of the genus *Arion* in Portugal on the basis of the anatomy of topotypes collected by systematic sampling.



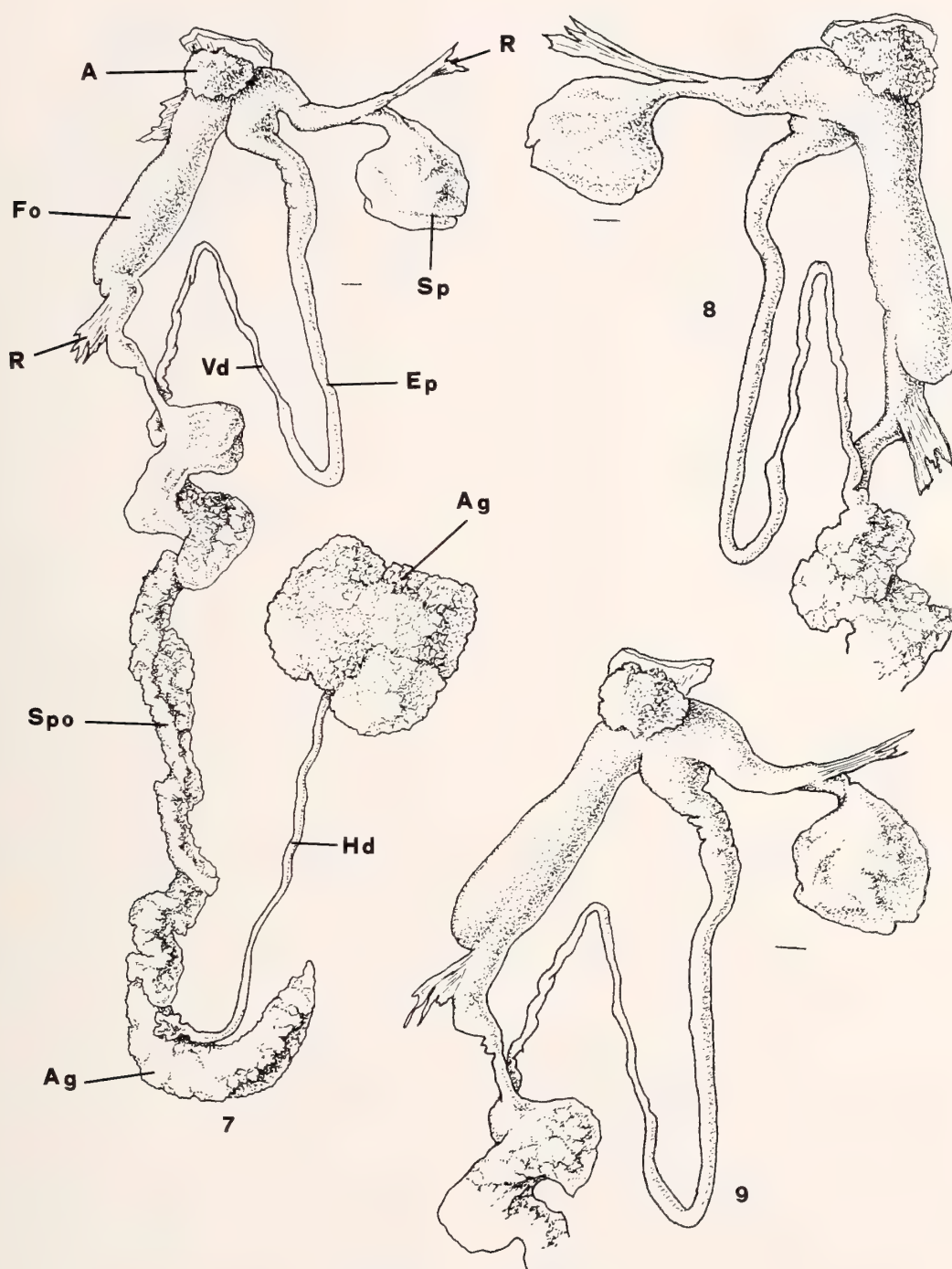
Explanation of Figures 4 to 6

Figures 4-6. *Arion flagellus*, Sierra del Gistral (Lugo). Figure 4. Organs *in situ*. Figure 5. Digestive tract. Figure 6. Pallial complex. Scale 1 mm.

Specimens of *Arion flagellus* (deposited in the collection of the Departamento de Biología Animal, Facultad de Biología, Universidad de Santiago, Spain) were collected in Galicia between 1979 and 1984 by standard methods for capture, transport, killing, fixation, and preservation. To record external morphology, the most representative specimens were photographed at the time of capture. External morphology and genitalia were drawn to scale using a camera lucida and a binocular magnifier. Copulation was drawn from slides taken *in situ* with no scale.

The following specimens sent by Dr. S. M. Davies were used for comparison: *Arion flagellus* from Bramley Bank, Croydon, England; *A. lusitanicus* collected in the garden of 63 Beechwood Road, South Croydon, Surrey, England; and *A. subfuscus* from Coulsdon Woods, Surrey, England. We also studied specimens of *A. subfuscus* collected to the north of Antwerp, Belgium, and sent by Dr. T. Backeljau.

In what follows, the morphology of the specimens we found in the northwest of Spain is described and compared with the English topotypes.



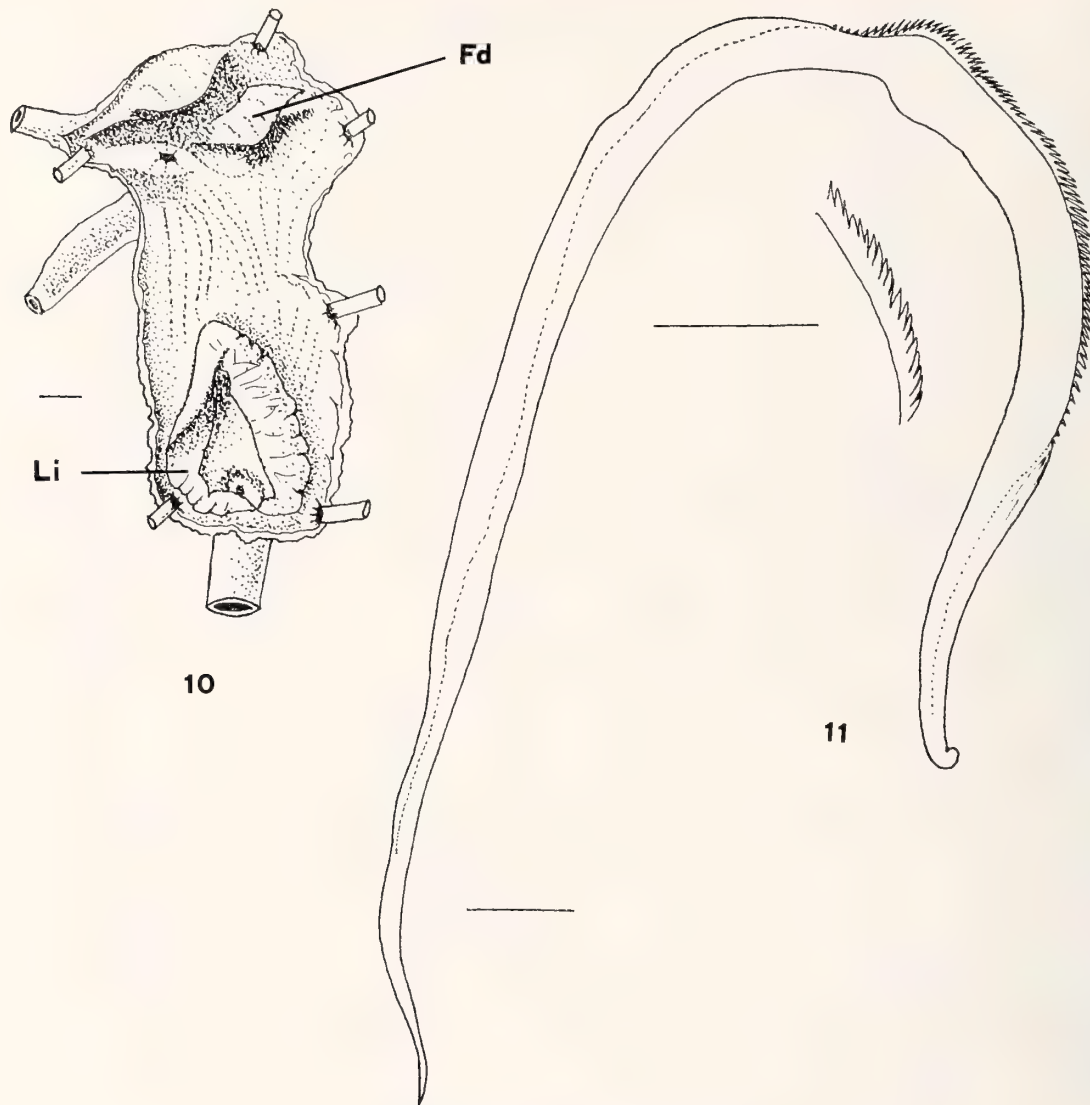
Explanation of Figures 7 to 9

Figures 7–9. *Arion flagellus*, Sierra del Gistral (Lugo). Various views of genitalia. Key: A, atrium; Ag, albumen gland; Ep, epiphallus; Fo, free oviduct; Hd, hermaphrodite duct; Ot, ovotestis; R, retractor muscle; Sp, spermatheca; Spo, spermoviduct; Vd, vas deferens. Scale 1 mm.

Arion flagellus Collinge, 1893

Material examined (Map 1): Sobrado de los Monjes (La Coruña), U.T.M. (Universal Transverse Mercator projection) = 29TNH76, 8 October 1979 (4 specimens). San-

tiago de Compostela (La Coruña), U.T.M. = 29TNH34, 14 October 1984 (23 specimens). Coto del Xirimbao (Vedra, La Coruña), U.T.M. = 29TNH43, 21 October 1984 (6 specimens). Ferreira de Valadouro (Lugo), U.T.M. = 29TPJ22, 17 September 1984 (20 specimens). Cuadramón



Explanation of Figures 10 and 11

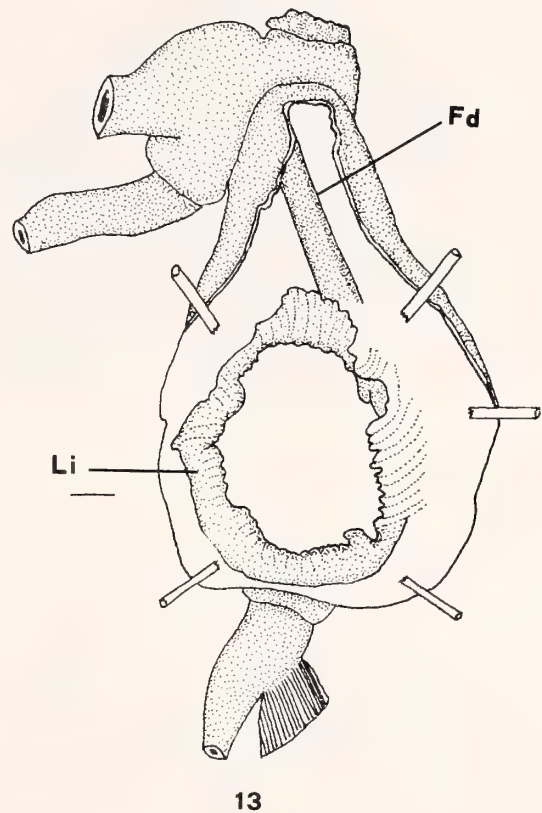
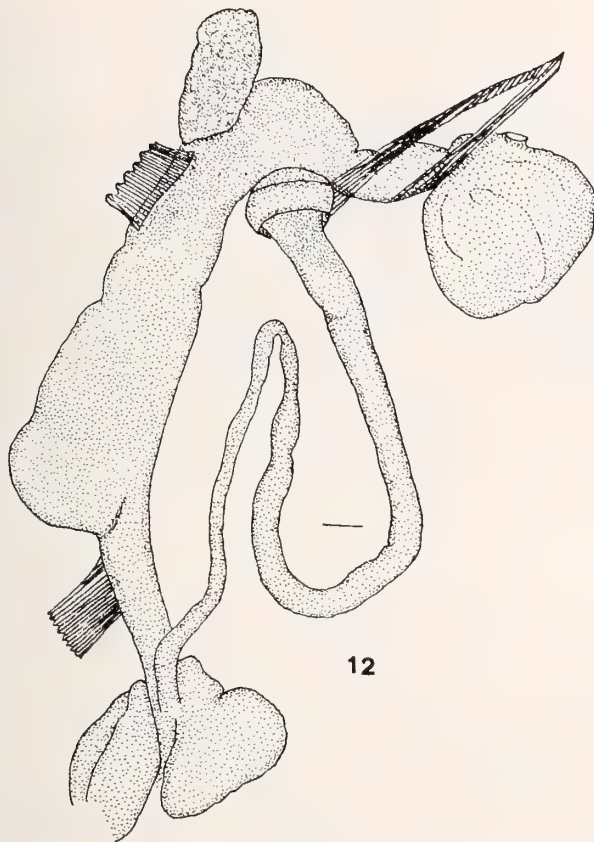
Figures 10 and 11. *Arion flagellus*, Sierra del Gistral (Lugo). Figure 10. Ligula. Figure 11. Spermatophore with detail of toothlets. Key: FD, fold; Li, ligula. Scale 1 mm.

(Sierra del Gistral, Lugo), U.T.M. = 29TPJ21, 18 October 1984 (13 specimens).

The species may be very abundant in Galicia, since most reports of *Arion lusitanicus* may in fact refer to *A. flagellus*. Specimens were found on acid soil over granite under vegetation dominated by pines, eucalyptus and, to a lesser extent, chestnut and birch.

Description: This is a large slug and the fully extended length in vivo can exceed 90 mm. In 70% alcohol, specimens shrink and measure 50 to 70 mm (Figures 1-3). The live body color is dark gray, with a greenish yellow or greenish chestnut flush (the green coloration of the Galician *Arion*

flagellus is striking enough for country folk in some places to refer to this species as the "green slug that lives in the meadows"); its flanks are lighter, greenish yellow predominating over the gray. The back and mantle of some specimens have two darker bands, the one on the right surrounding the pneumostome; like the flanks, the dorsal area between the bands is lighter. Juveniles are lighter colored than adults, with or without bands. In alcohol, juveniles and adults turn darker and the dorsal bands tend to disappear. The dermal tubercles are prominent, as in the Portuguese *A. lusitanicus*, forming longitudinal keels when the animal contracts. The foot fringe is greenish yellow or greenish orange and the lineoles (vertical lines) are black.



Explanation of Figures 12 and 13

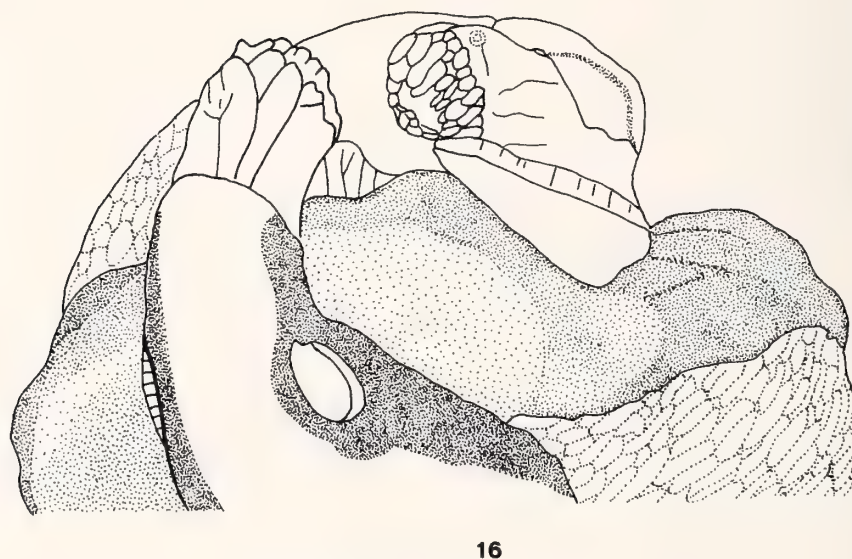
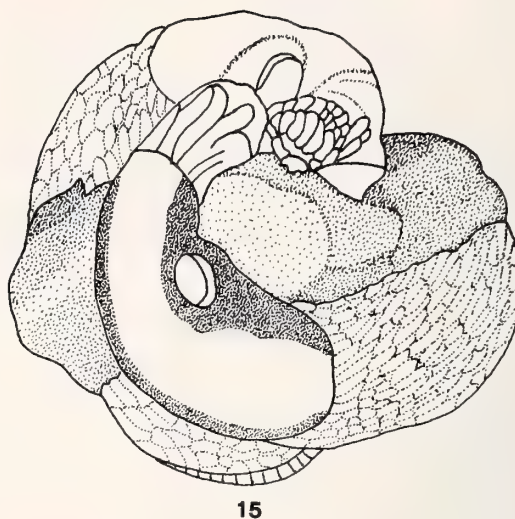
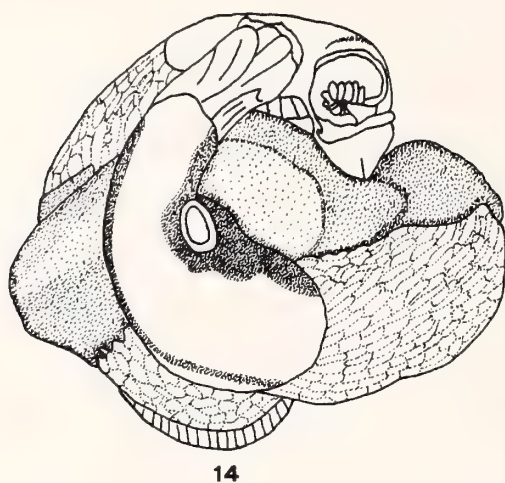
Figures 12 and 13. *Arion flagellus*, Santiago de Compostela (La Coruña). Figure 12. Genitalia. Figure 13. Ligula (stimulator organ). Key: Fd, fold; Li, ligula. Scale 1 mm.

The tentacles and the back of the head are black. Both adults and juveniles show a uniformly pale greenish yellow or greenish orange sole. The body mucus is whitish or colorless, turning a dirty white upon contact with alcohol; the sole mucus is orange. The limacella (internal shell) is formed of more or less aggregated calcareous grains.

Organs in situ (Figure 4). The digestive tract (Figure 5) and pallial complex (Figure 6) have the characteristic topography of the genus. The arteries feeding the digestive gland and tract are white in specimens from Ferreira de Valadouro and Cuadramón preserved in 70% alcohol.

Genitalia (Figures 7, 8, 9, 12). The ovotestis is voluminous and is made up of brown acini. The hermaphrodite duct is long and straight, and the albumin gland almond-shaped, somewhat curved in the middle. The spermoviduct is long and has no distinguishing color. The epiphallus measures 20–30 mm in adults containing a whole spermatophore, while in subadults and seniles it is only 14–25 mm in length; on the other hand, the vas deferens in these latter classes measures 10–18 mm, while in adults containing a whole spermatophore its length is 10–15 mm. The juvenile epiphallus is up to three times longer than

the vas deferens, both structures together measuring 13 mm or less. The junction between the vas deferens and the epiphallus is marked by a constriction, and the epiphallus has a strong, annular thickening at its entry into the proximal atrium. The distal free oviduct is as long as the vas deferens (half as long as the epiphallus), with a pronounced lateral dilation housing the ligula (stimulator organ); the proximal part of the distal free oviduct can have a lateral elbow. The proximal free oviduct is one-half the length of the distal free oviduct. The ligula (Figures 10, 13) possesses a circular or oblong shape, and is generally located in the proximal third of the distal free oviduct; in some specimens (Figure 13) there are one or two folds that continue to the proximal atrium, where they may give rise to a small dilation at the proximal end of the spermatheca duct. The orifice of the proximal free oviduct may open inside or outside the ligula. The spermatheca (bursa copulatrix) is spherical or pear-shaped, its duct being shorter than the epiphallus, with, in some specimens, a papilla located at the commencement of the duct and pointing towards the proximal atrium (Figure 10). The proximal atrium is small; and the distal atrium is



Explanation of Figures 14 to 16

Figures 14–16. *Arion flagellus*, Ferreira de Valadouro (Lugo). Copulation. Not to scale.

more or less spherical, covered externally by tissue of glandular appearance. The oviduct retractor muscle appears strongly united with the retractor of the bursa copulatrix, from which fascicles sometimes extend to the annular thickening of the epiphallus; in the inferior distal free oviduct, parietal muscles are sometimes united. No part of the genitalia has black pigmentation except the distal epiphallus near the annular ring (this pigmentation is not a result of preservation in alcohol, being found in live specimens).

Spermatophore (Figure 11). The spermatophore is cylindrical, and measures 20 mm long, tapering to a rounded

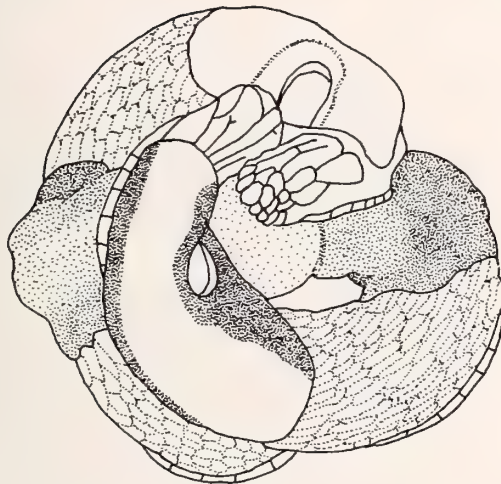
knob at one end and to a point at the other. Upon extraction it resumes the U-shape it has inside the genitalia after transfer. A longitudinal serrate crest with tall, narrow, closely packed teeth runs almost the whole length, dwindling at its ends to merge with the body of the spermatophore.

Copula (Figures 14–24). Copulating *Arion flagellus* were photographed on the night of 17 September 1984 at Ferreira de Valadouro (Lugo); relative humidity was close to 100%. The entire event was not witnessed, but certainly lasted at least 45 min.

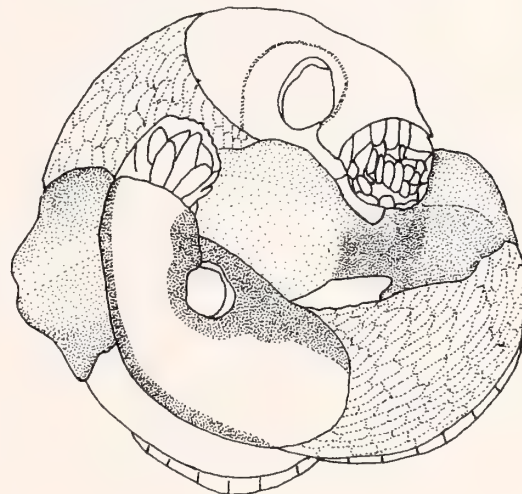
In the precopulation phase, the two individuals move



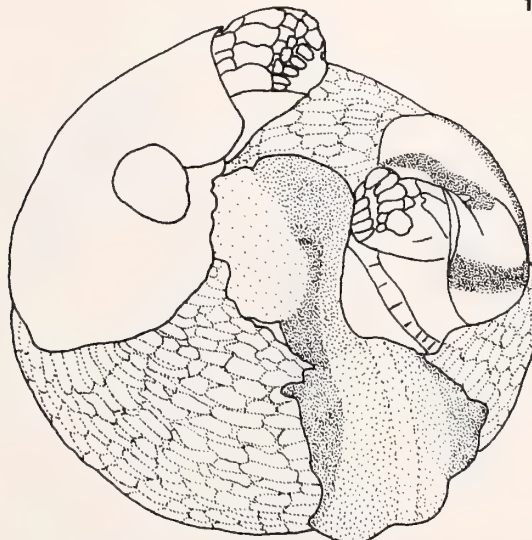
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18



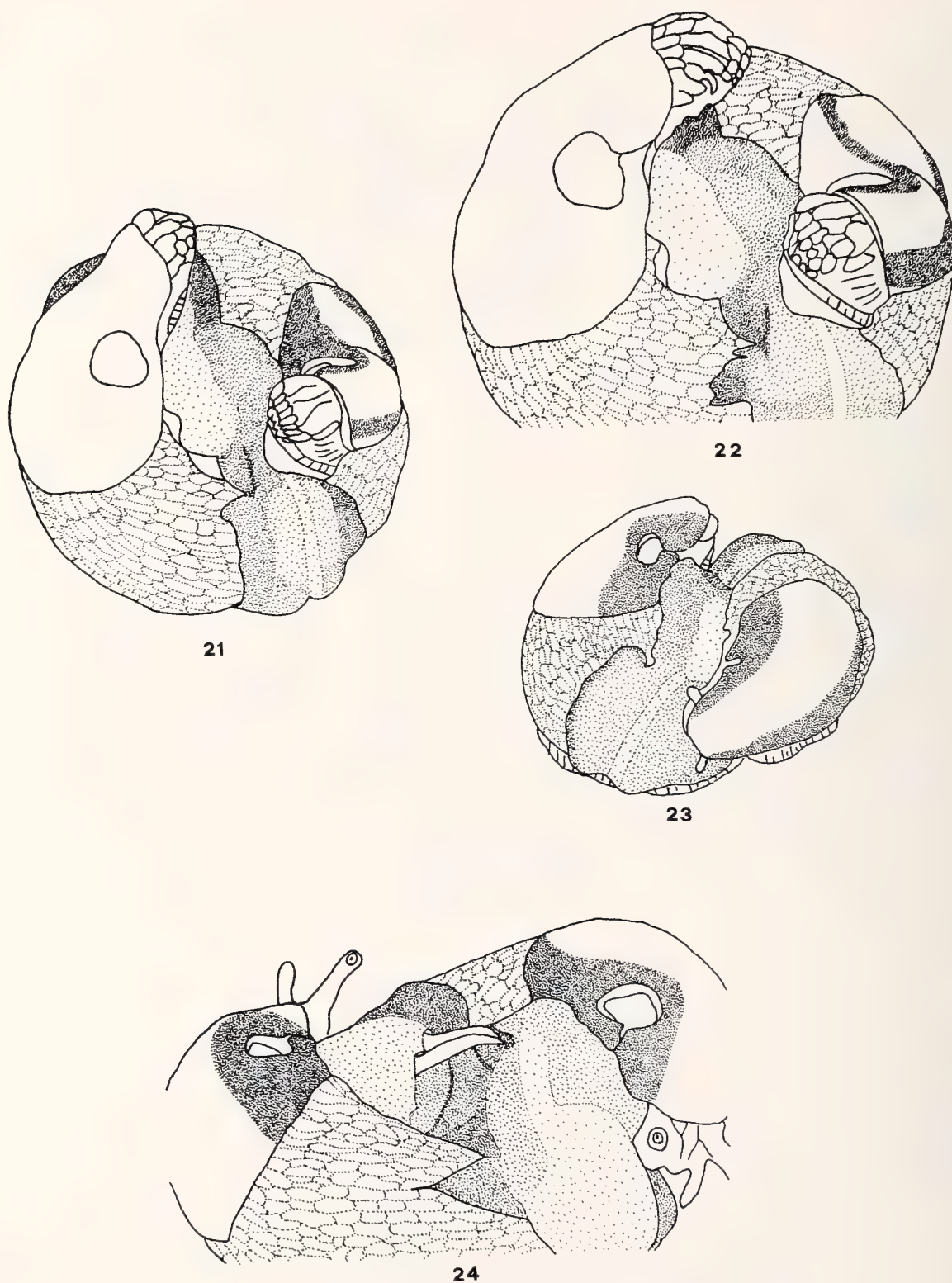
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20

Explanation of Figures 17 to 20

Figures 17–20. *Arion flagellus*, Ferreira de Valadouro (Lugo). Mutual licking phase of copulation. Not to scale.



Explanation of Figures 21 to 24

Figures 21-24. *Arion flagellus*, Ferreira de Valadouro (Lugo). Copulation, final phase. Not to scale.

one behind the other, the rear one licking the other's caudal area. They then curl into interlocking Cs with their genital orifices opposite each other, and shortly afterwards the posterior part of genitals (atrium and free oviduct) are evaginated or everted (Figure 14) together with the distal parts of the free oviduct and the ligulas, which grip the mate's tail (Figures 14, 15, 19). Copulation is static (in particular they do not move in circles), except that they often lift their heads, with the tentacles retracted, and lick or scrape the mate with the protracted mandible and radula (Figures 15, 16, 18). At the end of copulation (Figure 24), they begin to extend their tentacles and move away in opposite directions. At this point the amber-colored tips of the spermatophores are visible (Figure 24) and the ligulas are still evaginated. The two individuals separate and invaginate their genitalia very rapidly; once separated they curl up and lick the spot where the other had placed its ligula.

DISCUSSION

The dissected Galician specimens of *Arion flagellus* resemble the English specimens closely, the proportions of the various parts of the genitalia and the size and appearance of the spermatophore being identical. The main difference concerns copulation. DAVIES (1987) states that most of the evaginated anterior part of the genitalia of copulating English specimens lies underneath the animals, and cannot be seen until they start to separate; the evaginated anterior part of the genitalia of Galician *A. flagellus* lies between and upon the backs of the pair, with the ligulas visibly hugging the mate's body, a position resembling that of copulatory English *A. lusitanicus* in DAVIES' (1987) Figure 3B.

The Galician *Arion flagellus* is very like the Portuguese *A. fuliginus*. The two species are almost the same length, both may or may not have dorsal bands, and the sole is always white or yellowish. However, *A. fuliginus* never has the greenish flush that is characteristic of *A. flagellus*. The genitalia are also very similar (in particular, the relative proportions of the epiphallus and the vas deferens are the same), except that the ligula of *A. flagellus* is circular whereas that of *A. fuliginus* is shaped like an inverted V. The spermatophores are of equal length (20 mm), but that of *A. fuliginus* widens towards the middle, whereas that of *A. flagellus* has a more uniform cross section; furthermore, the spermatophore crest of *A. fuliginus* is not toothed or has less pronounced teeth than that of *A. flagellus*, and the spermatophore itself does not adopt the U-shape characteristic of *A. flagellus*. However, the two species differ mainly in their copulation. *A. fuliginus* places its ligula on the flanks of the mate, whereas the Galician *A. flagellus* places its ligula upon its mate's back, gripping it; and the rotation of the pair that occurs in the copulation of the Portuguese *A. fuliginus* is not performed by the *A. flagellus* of Galicia (though according to DAVIES [1987], English

specimens of both *A. subfuscus* and *A. flagellus* may slowly rotate when copulating).

Externally, the Galician *Arion flagellus* differs in color from the Portuguese *A. lusitanicus*, which when adult has a dark yellowish chestnut body with two dorsal bands and a sole that is dark gray or black peripherally and lighter centrally; the upper parts of juveniles may be greenish gray or black. Internally, the epiphallus of *A. lusitanicus* is the same length as the vas deferens, and the spermatophore is longer than in the Galician *A. flagellus* (40 mm vs. 20 mm). The two species also differ in their copulation behavior and the shape of the ligula.

The Portuguese *Arion nobrei* is much larger than the Galician *A. flagellus*, and is olive green or bronze colored. The sole is always black. The genitalia are much larger than in *A. flagellus*: the epiphallus measures 30–35 mm, and the spermatophore may exceed 65 mm.

The Galician *Arion flagellus* differs from the English and Belgian *A. subfuscus* in size. Internally, its epiphallus and vas deferens are twice as long as those of *A. subfuscus*.

The Galician *Arion flagellus* differs in both internal and external morphology from the English *A. lusitanicus*, which exceeds 100 mm in length and is black or brown, with a sole of the same color. The epiphallus of the English *A. lusitanicus* is the same length as the vas deferens (both 18–20 mm), the ligula is elliptical, and the spermatophore is longer than that of *A. flagellus* and has a different shape.

ACKNOWLEDGMENTS

We thank Miss S. M. Davies (U.K.) for supplying *Arion lusitanicus*, *A. subfuscus*, and *A. flagellus* for comparison, Dr. T. Backeljau (Belgium) for sending us specimens of *A. subfuscus*, and Drs. T. Rodríguez and A. Outeiro (Spain) for their help with the drawings of *A. flagellus*.

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NOTES, INFORMATION & NEWS

New Range Information for the Banana Slug

Ariolimax columbianus (Gould, 1851)

by

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A previously unreported locality for *Ariolimax columbianus* (Gould, 1851) in Plumas County, California, is herein documented. Los Angeles County Museum of Natural History (LACM) locality 89-38 is in the northernmost Sierra Nevada. Other Sierra Nevada localities have been reported by COOPER (1886) (Placer and Plumas [= Sierra] Counties), MEAD (1943) (Calaveras, El Dorado, Placer [= COOPER, 1886], and Tuolumne [= California Academy of Sciences (CAS) 078011 and 078034] Counties) and PILSBRY (1948) (Tuolumne County). A generalized locality map in HARPER (1988) included the localities of MEAD (1943) and PILSBRY (1948). COOPER (1886:253) reported "the abundance of some kinds of land molluscs has attracted the attention of the miners at one locality, called "Slug Cañon," in Plumas County" (Slug Canyon is actually located in Sierra County southwest of Downieville, California, ca. 1098 m elevation [S. Larson, personal communication, 1991; U.S. Geological Survey Downieville (PR 1975) 7.5' quadrangle]). Cooper included this information under the heading of "*Ariolimax Californicus*, J.G.C." [sic] [= *A. columbianus* (Gould, 1851) *fide* MEAD (1943)] and described it as "this great slug, apparently identical with the coast species." Unpublished Sierra Nevada records from the CAS Invertebrate Zoology collection for *A. columbianus* include Calaveras, Nevada, and Plumas Counties (E. Kools, personal communication, 1991).

The new LACM locality is in NW¼, SW¼, SE¼, section 26, T26N, R9E, U.S. Geological Survey Crescent Mills (1980) 7.5' quadrangle (40°04.3'N, 120°55.3'W) 2.75 km SW of Crescent Mills, Plumas County, California, at 1097 m elevation, 5 m upslope from Dixie Creek, a south-flowing tributary of Indian Creek on the property of Flora Berridge and Doris and Bruce Livingston. A single living specimen that measured 98 mm in length was collected by the author on 25 August 1989 and is preserved in 70% ethyl alcohol in the LACM Recent mollusk collection (LACM 89-38.4). This locality is significant in that it documents one of the highest elevations (1097 m) that *Ariolimax columbianus* has been collected and it extends its known range to the northernmost Sierra Nevada. Previ-

ously reported high elevation Sierra Nevada localities include: 1128 m near Alta, Placer County and ca. 1098 m near Downieville, Sierra County (COOPER, 1886); and ca. 985 m near Riverton, El Dorado County (MEAD, 1943). Unpublished high elevation localities from the CAS collection include CAS 077204 and 077215 1174 m at Rich Gulch, Plumas County.

The author was alerted in 1988 to the presence of *Ariolimax columbianus* in Plumas County by the property owners, who had observed this species as early as 1976; however, sightings since 1989 have been rare. Other molluscan taxa associated with this locality are juvenile *Pristoloma* sp. and *Vespericola sierranus* (Berry, 1921). A Dixie Creek stream-side leaf-litter sample (LACM 89-37) yielded the introduced species *Oxychilus alliarius* (Miller, 1822). A subsequent re-collection of these localities was made on 26 November 1989. LACM 87-107 (= LACM 89-38 in locality only) yielded *Vitrina alaskana* Dall, 1905, and the introduced species *Oxychilus draparnaldi* (Beck, 1837). A leaf-litter sample from LACM 89-108 (= LACM 89-37 in locality only) yielded *Vitrina alaskana* Dall, 1905, *Vespericola sierranus* (Berry, 1921), and *Helminthoglypta proles* (Hemphill, 1892).

Acknowledgments

Special thanks to Flora Berridge and Doris and Bruce Livingston for reporting the presence of *Ariolimax columbianus* on their property. Thanks to Elizabeth Kools (CAS) and Paul Scott (Santa Barbara Museum of Natural History) for providing timely locality information. Scott Larson (Plumas County Museum, Quincy, California) and Lois M. Schenk kindly provided historical information. C. Clifton Coney and James H. McLean (LACM), Barry Roth (University of California, Museum of Paleontology), and an anonymous reviewer critiqued the manuscript.

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Use of Gonad Color in Sexing Broodstock of
Placuna placenta (Linnaeus, 1758)

by

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Introduction

The windowpane oyster, *Placuna placenta* (Linnaeus, 1758), is a highly valuable bivalve species inhabiting the muddy bottom of coastal bays from the Arabian Sea on the west through the Indian Ocean and Malayan Seas to the coast of China on the east (HORNELL, 1909). In the Philippines, *P. placenta* is extensively collected from the wild because of the high demand for its translucent shell, which is fashioned into various articles exported to the United States and Europe. As a result of overharvesting, *P. placenta* populations in some natural beds are already depleted. Therefore, there is a need to conserve this resource through aquaculture. Hatchery techniques should be developed to produce seeds for reseeded and farming purposes.

At the Aquaculture Department of the Southeast Asian Fisheries Development Center (SEAFDEC/AQD), *Placuna placenta* has been induced to spawn by water flow manipulation (YOUNG, 1980). Other methods such as the addition of gametes, temperature shock, and salinity shock are presently being tried. With these induced spawning methods, there is a need to have a high degree of certainty as to the sex of the animal being used. Further, it is important that the method of sexing does not involve sacrificing the animal. However, it has been reported that sexes in *P. placenta* can be determined only by gonad histology. ROSELL (1979) stated that male and female *P. placenta*, which are dioecious, are distinguishable upon histological examination of the gonads, but they are without apparent sexual dimorphism. MAGSUCI *et al.* (1980) reported that the sex of *P. placenta* cannot be differentiated except by microscopic examination. Nevertheless, if gonad color, as seen through the translucent shell, could be proven to be a highly reliable basis for sexing, then this method would be useful in broodstock selection. Therefore, this study was conducted to investigate the use of gonad color for sexing *P. placenta* broodstock.

Materials and Methods

A total of 80 *Placuna placenta* individuals (64–135 mm) collected in the months of October 1989 and February and May 1990 from Pilar, Capiz, Philippines, by commercial skin divers were used in this study.

The color of the gonad was determined by viewing the animal against a light and classified either as orange or cream, for female or male, respectively.

Gonads were dissected, fixed in 10% formalin, dehydrated in different grades of alcohol (70–100%), cleared in toluene, and embedded in 56°C paraffin wax. Sections of 4–5 μ m thickness were cut and stained with hematoxylin and eosin (BELL & LIGHTNER, 1988).

Gonad sections were examined with an Olympus microscope and the sex and gonadal stage determined on the basis of the categories used by ROSELL (1979).

Results of the histological sex identification were then compared with gonad color to determine the reliability of gonad color as a basis for sexing.

Results and Discussion

The number of specimens in which gonad color corresponded to sex, or did not correspond, were, for several gonad stages: immature, 10 vs. 4; early active, 6 vs. 1; late active, 25 vs. 0; ripe, 15 vs. 0; partially spawned, 6 vs. 3; spent, 9 vs. 1.

Among the 28 samples in October 1989, wherein 50% had immature gonads, 25% partially spawned to spent gonads, and only 3.67% ripe, the level of accuracy in matching gonad color with the correct sex was only 78.57%. On the other hand, in the February and May 1990 samples, having no immature individuals but a high percentage (71.97%) of individuals in the late active and ripe gonad stage, the level of accuracy was 90.91% and 96.67%, respectively.

Histological analysis of the gonad confirmed the sex of the animal. Overall, a high percentage (88.75%) of the samples matched in gonad color and sex, cream for male and orange for female. The unmatched 11.25% of the samples were either in the immature, early active, partially spawned, or spent gonad stages.

These findings show that gonad color can be used as a basis for sexing *Placuna placenta* with ripe gonads. It is not, however, as highly reliable in individuals with immature, partially spawned, or spent gonads.

Gonad color is also an indication of the animal's sexual maturity and readiness to spawn. If the color difference is distinct, then the animal is mature or ripe and can be easily induced to spawn. Therefore, in breeding *Placuna placenta*, those with distinct gonad color (cream or orange) should be chosen. Breeding attempts with this economically important bivalve species at SEAFDEC/AQD now make use of this method of sexing in broodstock selection.

This sexing method becomes limited by the thick and opaque shell that develops as a result of old age (MAGSUCI *et al.*, 1980) and makes it difficult to ascertain the gonad color externally.

Acknowledgments

Thanks are due to Attorney R. Panique and Mrs. N. P. Vardeleon of Polyshell Inc., Philippines, for providing the *Placuna placenta* samples; G. Erazo, S. Torrento, and F. Torreta for the gonad histological preparation; and Prof.

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International Commission on Zoological Nomenclature

Comment or advice on applications to the ICZN is invited for publication in the *Bulletin of Zoological Nomenclature* and should be sent to the Executive Secretary, ICZN, % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

The following applications and opinions were published on 26 March 1991 in Vol. 48, Part 1, of the *Bulletin*:

- Case 2736—*Haustator* Montfort, 1810 (Mollusca, Gastropoda): proposed conservation by suppression of *Aculea* Perry, 1810, an unused senior subjective synonym.
- Case 2769—*Laecochlis* Dunker & Metzger, 1874 (Mollusca, Gastropoda): proposed conservation as the correct spelling.
- Case 2732—*Ceratites nodosus* (Cephalopoda, Ammonoidea): proposed attribution of the specific name to Schlotheim, 1813, and proposed designation of a lectotype.

Opinion 1623—*Risomurex* Olsson & McGinty, 1958 (Mollusca, Gastropoda): *Ricinula deformis* Reeve, 1846, designated as the type species.

The following applications and opinions were published on 30 September 1991 in Vol. 48, Part 3, of the *Bulletin*:

- Case 2710—Clavidae McCrady, 1859 (Cnidaria, Hydrozoa) and Clavinae Casey, 1904 (Mollusca, Gastropoda): proposal to remove the homonymy by changing the molluscan subfamily name to Clavusinae.
- Case 2766—*Conus fulmen* Reeve, 1843 (Mollusca, Gastropoda): proposed conservation by suppression of its unused senior subjective synonym *C. modestus* Sowerby, [1833]. And *Conus berghausi* Michelotti, 1847: proposed precedence over *C. demissus* Philippi, 1836.
- Opinion 1650—Cymatiinae Iredale, 1913 (1854) (Mollusca, Gastropoda) and Cymatiinae Walton in Hutchinson, 1940 (Insecta, Heteroptera): homonymy removed.
- Opinion 1651—*Mytilus anatinus* Linnaeus, 1758 (Currently *Anodonta anatina*; Mollusca, Bivalvia): neotype designation confirmed.

Student Research Grant in Malacology

The Western Society of Malacologists and a coalition of western United States shell clubs have announced the availability of grants to support student research in malacology. Funds are available for actual research costs, including but not limited to field and laboratory equipment, chemicals, photographic supplies, computer time and supplies, microscope usage fees, and reasonable research travel costs. One or more research grants up to \$1500 are available.

To be eligible, an applicant must be a full-time student in a formal graduate or undergraduate degree program. The research project must be focused primarily on the systematics, biology, ecology, physiology, biochemistry, or paleontology of marine, terrestrial, or freshwater mollusks.

Completed applications must be received no later than **15 May 1992**. For more information and an application send a self-addressed, stamped (if residing in U.S.) envelope to: Malacology Grant, Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105, USA.

BOOKS, PERIODICALS & PAMPHLETS

Economic Zoology: A Dictionary of Useful and Destructive Animals

by B. JANGI. 1991. A. A. Balkema Publishers, P.O. Box 1675, Rotterdam, The Netherlands. Hardback. 216 pp. Price: \$63.00

Attracted to this book by an illustration of a giant squid on the cover, I asked for a review copy. The accompanying advertisement described the book as "the first attempt of its kind, resulting in a miniature encyclopaedia on economic zoology. From amoebas to apes it spans about 1,500 entries." By "economic zoology" is meant the benefits (uses) and losses to humans caused by animals and animal products. The dictionary entries briefly address various animal groups, pathological conditions afflicting them, and economic practices employed.

Although the book is aimed, according to the author, at researchers in biological sciences, the book is more likely to serve a more generalist audience. Someone reading an article on silkworms in China in a popular science magazine might be interested in the fact that the silk of bombycids is secreted as a single continuous fiber some 800–1200 m long, or the reader might find useful the definition of "frass: silkworm waste used as fish food and fertilizer

in China." A specialist, however, is not likely to find in the book much new in his or her field.

Most malacologists probably would not be impressed with the fewer than 30 substantive entries concerning mollusks (some additional listings are simple cross-references). Although the entries extend from abalone to *Zirfaea*, in total the material on mollusks occupies about five pages only. One of these is devoted to "shellfish farming" and most of the rest are found under the class-level headings of Cephalopoda, Gastropoda, and Pelecypoda. Rabbits receive treatment about equal to that of gastropods.

A more generally worrisome feature of the book is some out-of-date information and illustrations of poor quality. For example, the cephalopod and pearl-farming entries cite annual catch figures from the 1960s only, and several of the already sparse illustrations are from pre-1960 editions of Ralph Buchsbaum's *Animals without Backbones*.

Economic Zoology does contain some useful and interesting entries, and perhaps larger libraries should have a copy. But the \$63 price tag is far too dear for the potential benefits that most individuals might receive—another form of economic zoology.

D. W. Phillips

Manuscripts

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The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

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c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

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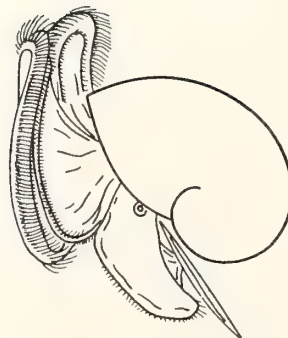
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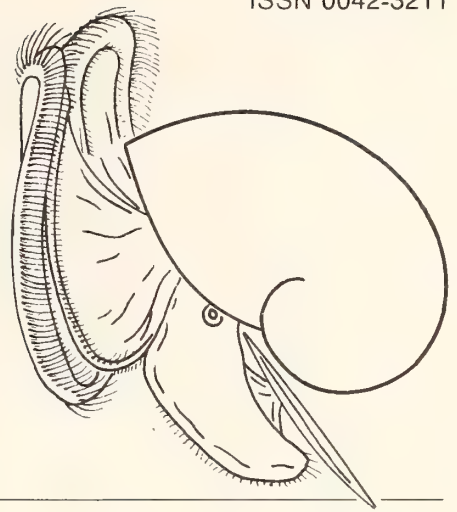
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The Veliger is open to original papers pertaining to any problem concerned with mollusks.

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Humoral Immunity: α_2 -Macroglobulin Activity in the Plasma of Mollusks

by

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Abstract. The α_2 -macroglobulins are protease-binding proteins that shield bound proteases from active site protease inhibitors of suitably high molecular mass. The active site of the bound protease is unaffected, and the bound enzyme remains able to hydrolyze low molecular mass amide and ester substrates. The ability to protect the amidolytic activity of trypsin from the high molecular mass inhibitor soybean trypsin inhibitor was used to demonstrate an α_2 -macroglobulin-like activity in the hemolymph of representatives of bivalve and gastropod mollusks and blood of the cephalopod *Loligo pealii*. This is the first documentation of the presence of α_2 -macroglobulin-based systems of immunity in mollusks.

INTRODUCTION

Proteases are involved in physiological processes such as blood clotting and in pathological processes such as neoplastic invasion, inflammation, and invasion by pathogenic microorganisms and multicellular parasites. Since extracellular proteases in the internal milieu may be quite destructive, animals have evolved regulatory processes for their inactivation and removal. Most important are the peptide protease inhibitors. Members of the α_2 -macroglobulin class of protease inhibitors act by the unique mechanism of a physical folding of the peptide chains of α_2 -macroglobulin around the protease molecule to form a "cage" that sterically blocks interaction of the protease with large molecules in the surrounding milieu (STARKEY & BARRETT, 1973). Amide and ester substrates small enough to diffuse into the cage can still be hydrolyzed since the active site of the entrapped protease is unaffected. α_2 -

Macroglobulin is a major protein in mammalian plasma and has been proposed to function as an important scavenger of proteases from the blood and tissue fluids (for reviews see FEINMAN, 1983; SOTTRUP-JENSEN, 1987).

A specific assay for α_2 -macroglobulin derives from the ability of α_2 -macroglobulin to protect trypsin from active site inactivation by soybean trypsin inhibitor (SBTI)¹ (GANROT, 1966; ARMSTRONG *et al.*, 1985). To detect α_2 -macroglobulin in a sample, the sample is reacted sequentially with saturating concentrations of trypsin and then with the high molecular mass active site inhibitor SBTI. SBTI inactivates all free trypsin but fails to interact with α_2 -macroglobulin-bound trypsin. When a low molecular mass trypsin substrate is then added, the rate of substrate hydrolysis is a measure of the α_2 -macroglobulin-bound trypsin, and thus of α_2 -macroglobulin. In this report, we use this assay to document the presence of α_2 -macroglob-

ulin in the plasma of members of three classes of mollusks: the gastropod *Busycon canaliculatum* (Linnaeus, 1758), the bivalve *Spisula solidissima* (Dillwyn, 1817), and the cephalopod *Loligo pealii* Lesueur, 1821.

MATERIALS AND METHODS

Recently collected animals were obtained from the Marine Resources Center of the Marine Biological Laboratory. Hemolymph was obtained from the different species as follows: *Busycon*: large individuals were induced to express all seawater from the mantle cavity by repeatedly poking the foot. The margins of the shell were then removed to expose the foot, which was cut with a scalpel blade, and the hemolymph was collected in a beaker. *Spisula*: hemolymph was aspirated from the marginal sinus with a 10 mL syringe and a 19 ga needle. *Loligo*: blood was collected from the heart or the post-cardiac sinus with a 3 mL syringe and a 23 ga needle. The hemolymph from all three species was centrifuged to remove the blood cells, and the hemocyanin in the plasma of *Busycon* and *Loligo* was removed by precipitation with 3% polyethylene glycol (PEG)¹. To avoid the formation of precipitates during the assay, the plasma of *Spisula* was dialyzed into 50 mM Tris, pH 8.1. The 3% PEG supernatant of *Busycon* hemolymph was exposed to 10% PEG and the precipitate was redissolved in 50 mM Tris, pH 8.1. No precipitate formed during the assay of the 3% PEG supernatant of *Loligo* blood, so this was assayed directly.

The various samples were measured into individual 1 mL plastic spectrophotometer cuvettes with 50 mM Tris buffer, pH 8.1 as the diluent to a final volume of 1080 μ L. Bovine pancreatic trypsin (Sigma cat. No. T-8003; 51% active, as determined by titration with p-nitrophenyl-p'-guanidobenzoate hydrochloride [CHASE & SHAW, 1967]) was then added and the sample was incubated for 10 min, room temperature. Excess SBTI was then added to inactivate all unbound trypsin. The amidolytic activity of the bound trypsin was determined spectrophotometrically by the rate of hydrolysis of N α -benzoyl-DL-arginine p-nitroanilide (BAPNA). In the absence of α_2 -macroglobulin, the SBTI completely blocked the hydrolysis of BAPNA. This assay is specific for α_2 -macroglobulin. To determine if α_2 -macroglobulin from selected mollusks was of the class whose activity requires the presence of a reactive internal thiol ester, inactivation with methylamine was attempted. Samples were treated overnight at room temperature with 0.2 M methylamine in 0.1 M Tris buffer, pH 8.1 as described previously (ARMSTRONG *et al.*, 1985), with parallel samples exposed to 0.1 M Tris buffer lacking methylamine as controls.

¹ Abbreviations: BAPNA = N α -benzoyl-DL-arginine p-nitroanilide; PEG = polyethylene glycol; SBTI = soybean trypsin inhibitor.

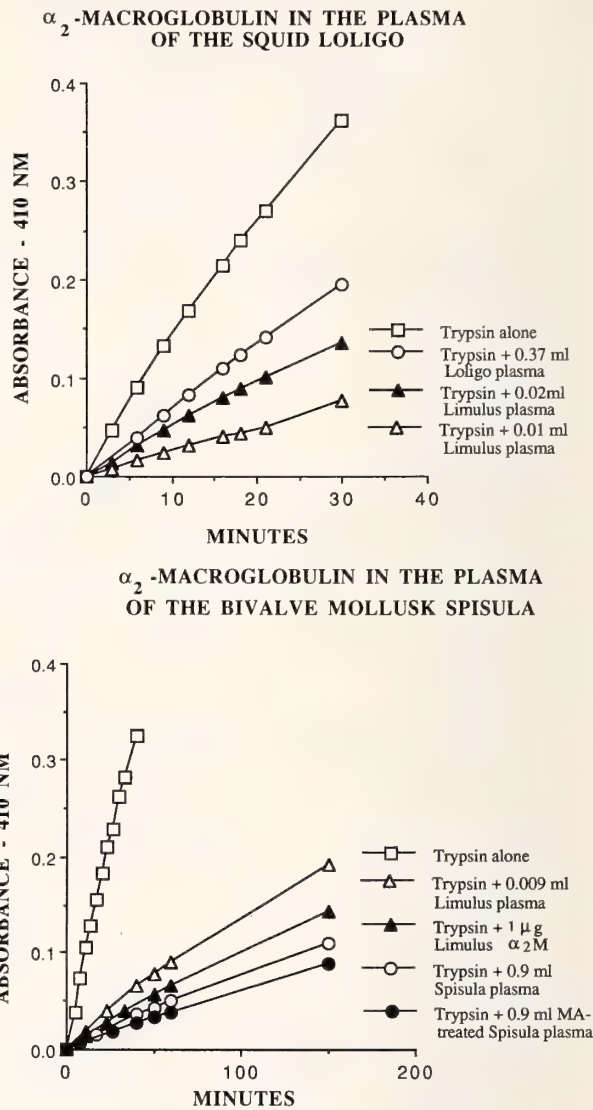


Figure 1

Protection of the amidase activity of trypsin by α_2 -macroglobulin in the plasma of mollusks. The plasma of the arthropod *Limulus polyphemus* was used as an internal standard since the form of α_2 -macroglobulin of this organism has been extensively characterized (ARMSTRONG & QUIGLEY, 1991). The plasma of the squid *Loligo pealii* (Figure 1a), contained about 7.7% of the α_1 -macroglobulin activity relative to that found in the plasma of *Limulus*, whereas the plasma of the bivalve *Spisula solidissima* (Figure 1b) contained lower levels of α_2 -macroglobulin. All samples of Figure 1a contained 5 μ g of active trypsin and those of Figure 1b contained 2.5 μ g.

RESULTS AND DISCUSSION

The three mollusks tested in the present study for α_2 -macroglobulin using the SBTI protection assay all showed α_2 -macroglobulin activity in the plasma, with *Loligo* show-

Table 1
 α_2 -Macroglobulin activity in the plasma of
 representative mollusks.

Genus	Treatment of plasma	μg of trypsin pro- tected/ mL
<i>Loligo</i>	none	6.4
<i>Spisula</i>	none	0.20
<i>Spisula</i>	methylamine	0.17
<i>Busycon</i>	3–10% PEG cut; $\times 20$ concentrated	0.25

ing the highest activity and *Busycon* the lowest (Table 1, Figure 1a, b). α_2 -Macroglobulin activity in whole hemocyanin-free plasma of *Busycon* was present at too low a level for direct detection but could be assayed following a 20-fold concentration of the high molecular mass proteins by precipitation with 10% PEG.

Two categories of α_2 -macroglobulin have been described: the thiol ester class, which possesses a reactive internal thiol ester bond that is hydrolyzed during reaction with proteases (reviewed in SOTTRUP-JENSEN, 1989), and the ovostatin class, which lacks the thiol ester (NAGASE & HARRIS, 1983; NAGASE *et al.*, 1983). Both classes of α_2 -macroglobulin bind proteases, and members of the two classes show significant amino acid sequence homology. A diagnostic feature of the thiol ester class of α_2 -macroglobulin is susceptibility to inactivation by small primary amines such as methylamine (BARRETT *et al.*, 1979; SWENSEN & HOWARD, 1979; ARMSTRONG & QUIGLEY, 1987), which act by direct attack on the thiol ester bond (TACK, 1983). The α_2 -macroglobulin activity of *Spisula* was resistant to methylamine under conditions where *Limulus* plasma suffered 95% inactivation (Figure 1b, Table 1), suggesting that *Spisula* α_2 -macroglobulin may lack a thiol ester bond that is necessary for activity. Unfortunately, the low quantity of α_2 -macroglobulin in the plasma of *Spisula* has frustrated our attempts to purify the protein and subject purified preparations to other tests for the presence of the thiol ester (*cf.*, ARMSTRONG & QUIGLEY, 1987; SPYCHER *et al.*, 1987).

Homologues of vertebrate α_2 -macroglobulin have recently been described from chelicerate (QUIGLEY & ARMSTRONG, 1983, 1985) and mandibulate (ARMSTRONG *et al.*, 1985; HERGENHAHN & SÖDERHÄLL, 1985; SPYCHER *et al.*, 1987) arthropods. These molecules share numerous functional properties with mammalian α_2 -macroglobulin and have notable identity at the level of peptide sequence in key functional domains (SPYCHER *et al.*, 1987; HALL *et al.*, 1989; SOTTRUP-JENSEN *et al.*, 1990). Here we report that α_2 -macroglobulin-like proteins are present also in the blood of representatives of three classes of mollusks.

The true physiological functions of the α_2 -macroglobulins are unclear even in vertebrates, which have been extensively studied in this regard. It seems likely that one function is the scavenging of proteases (SOTTRUP-JENSEN, 1987). α_2 -Macroglobulin has also been discovered to bind a variety of growth factors, suggesting that it may serve as a messenger molecule for the delivery of cytokines to the appropriate cellular targets (JAMES, 1990). It also has recently been reported that α_2 -macroglobulin functions in a complement-like hemolytic pathway in the horseshoe crab, *Limulus* (ENGHILD *et al.*, 1990). It is anticipated that a comparative study of α_2 -macroglobulin in a variety of phyla will illuminate its true function. Its presence in mollusks suggests that its involvement in immunity is important enough to have ensured its retention for the one-half billion years of evolution that separates the divergence of the vertebrate and mollusk lineages.

ACKNOWLEDGMENTS

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Laevipilina antarctica and *Micropilina arntzi*, Two New Monoplacophorans from the Antarctic

by

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Abstract. Two new monoplacophoran species, *Laevipilina antarctica* and *Micropilina arntzi*, are described from a depth of 191–742 m in the Lazarev Sea and eastern Weddell Sea. *Laevipilina antarctica* closely resembles the previously described species of *Laevipilina* McLean, 1979, and differs mainly in the convexity of the shell and in minor details of radular morphology. The stomach and the intestine of *L. antarctica* contained fine bottom sediment. The specimens range in length from 1.2 to 3.0 mm and the number of leaflets on the gills increases during ontogeny. *Micropilina arntzi* is the first live-taken species of its genus, and it is also the smallest known monoplacophoran, with a maximum shell length of 0.92 mm. It broods the young in the distal part of the oviduct and the pallial groove, and they are born at a size of 300 μ m shell diameter. Both species were found on sediment bottoms with stones and shells, on which they evidently live.

INTRODUCTION

The number of known Recent species of the class Monoplacophora has slowly but steadily risen since the first discovery of a living species by the *Galathea* Expedition in 1952. The number has now reached 17, and we list them (Table 1) and plot their distribution (Figure 1). In addition, there are a few records of unidentified specimens that are also mapped.

The specimens reported here are the first records of Monoplacophora from Antarctica. ROSEWATER (1970) reported an undescribed species from the Scotia Ridge (54°44'S, 55°33'W; Figure 1, number 6), southeast of the Falkland Islands, in 1647–2044 m depth. This locality is, however, separated from the Antarctic continental rise by depths exceeding 3000 m. We have examined this specimen (U.S. National Museum of Natural History, Division of Mollusks, No. 680431): it does not belong to *Laevipilina* or *Micropilina*, but seems to be a young specimen, perhaps of *Neopilina*, since the prismatic layer has a primarily radial orientation, rather than the neatly concentric arrangement of conspicuous prisms typical for *Laevipilina*.

FILATOVA *et al.* (1975) reported *Neopilina* sp. from the same area (56°29'S, 50°51'W; Figure 1, number 3) at 4664–5631 m depth. This specimen was later described as *Neopilina (Lemcheephyala) rebainsi* Moskalev *et al.*, 1983. That record is, however, also from north of the Antarctic continental rise.

Two specimens of the *Laevipilina* species described herein were found attached to rocks, but most of these and all specimens of the new *Micropilina* species were recovered from sorting sediment samples that had been sieved on board the R/V *Polarstern*, on a 0.5-mm-mesh sieve, and preserved in 95% ethanol. This explains the rather poor preservation of most specimens. Preservation in 10% formalin, buffered with 10 g of sodium-tetraborate per liter sample volume and added to the final sample, would have given a better result, especially if the container had been shaken a few times during the first two or three days.

The discovery that *Micropilina arntzi* is a brooder does not give any clues about the larval development of other monoplacophorans of which the apical area has been il-

Table 1
Distribution of Recent Monoplacophora.

No.	Species name and references†	Condi- tion‡	Locality	Depth (m)	Size (mm)
1	<i>Neopilina galathea</i> Lemche, 1957	1	Off Costa Rica, 09°23'N, 89°32'W	3591	29–37
	MENZIES & LAYTON 1962	1	Off Costa Rica, 10°07'N, 89°50'W	3718	
2	<i>N. bruuni</i> Menzies, 1968	1	Off Peru, 08°54'S, 80°41'W	4823–4925	15
3	<i>N. rebainsi</i> Moskalev et al., 1983	1	SE of Falkland Is., 56°29'S, 50°51'W	4664–5631	18
4	<i>N. sp.</i>	1	Off Peru, 08°46'S, 80°44'W	3909–3970	
	MENZIES (1968)	1	Off Peru, 11°30'S, 79°25'W	6146–6354	
		1	Off Peru, 08°52'S, 80°47'W	6313–6146	
5	<i>N. sp.</i>	1	Off N Chile, 23°50.0'S, 71°06.0'W	4600	5
	MOSKALEV et al. (1983)				
6	<i>N. sp.</i>	1	SE of Falkland Is., 54°44'S, 55°33'W	1627–2044	2.3
	ROSEWATER (1970)				
7	<i>Adenopilina adenensis</i> (Tebble, 1967)	1, r	Off South Yemen, 13°50'N, 51°47'E	3950–3000	10.7
8	<i>Vema ewingi</i> (Clarke & Menzies, 1959)	1	Off Peru, 07°35'S, 81°24'W	5817–5834	25
		1	07°30'S, 81°25'W	5841–5854	
		1	10°13'S, 80°05'W	6324–6329	
		1	12°02'S, 79°08'W	5607–5614	
	MENZIES (1968)		Off Peru, 08°25'S, 81°05'W	6260–6052	
			08°20'S, 81°04'W	6260–6364	
			08°16'S, 81°05'W	6156–6489	
			11°30'S, 79°25'W	6146–6354	
			08°10.5'S, 81°08.1'W	6002	
9	<i>Vema bacescui</i> (Menzies, 1968)	1	Off Peru, 08°44'S, 80°45'W	5986–6134	28
10	<i>Laevipilina hyalina</i> (McLean, 1979)	1	Off California, 32°41'N, 119°32'W	174–384	3
11	<i>L. rolani</i> Warén & Bouchet, 1990	1	Off Spain, 42°52'N, 11°51'W	985–1000	2
12	<i>L. antarctica</i> Warén & Hain, herein	1, r	Weddell and Lazarev seas, Antarctica	210–644	3.0
13	<i>Rokopella oligotropha</i> (Rokop, 1972)	1	Mid-Pacific, 30°05'N, 156°12'W	6065–6079	2.6
14	<i>R. zogradi</i> (Dautzenberg & Fischer, 1896)	d	Azores	1385–1600	3.7
	CESARI et al. (1987)	d	Mediterranean, NE of Corsica	180–500	
	CESARI et al. (1987)	d	Mediterranean, E of Sardinia	480–900	
15	<i>R. goesi</i> (Warén, 1988)	d	Caribbean, Virgin Islands	360–540	1.7
16	<i>R. veleronis</i> (Menzies & Layton, 1963)	1	Baja California, 27°52'N, 115°45'W	2730–2769	2.6
17	<i>Micropilina minuta</i> Warén, 1989*	d	Iceland, 63°23'N, 13°25'W	770–926	1.0
18	<i>M. tangaroa</i> Marshall, 1990	d	N of New Zealand, 31°31'S, 172°50'E	1216–1385	1.5
19	<i>M. arntzi</i> Warén & Hain, herein	1, d	Lazarev Sea, Antarctica	191–765	2.6
20	<i>Monoplacophorus zenkewitchi</i> Moskalev et al., 1983	1, r	W of Hawaii, 20°41.7'N, 170°52.9'W	2000	4.8

† "Author comma date" indicates original description and records therein; "REFERENCE (date)" are additional records.

‡ 1—found alive; d—only shells found; r—found attached on rocks.

* Also known as a Pleistocene fossil from deep-water deposits in Reggio Calabria, southern Italy (TAVIANI, 1990).

illustrated (WARÉN 1988, 1989), although it seems likely that *M. minuta* also is a brooder, judging from the similar shape and size (340 μ m) of the apical area.

Specimens of the two new species are at present being investigated anatomically by G. Haszprunar (Innsbruck).

Recently it has been advocated, especially in the paleontological literature (see, for example, PEEL [1991] and references therein), that the name Monoplacophora should be abandoned. The reason given is that the concept of the name has changed considerably since its introduction.

The name Monoplacophora was introduced by Odhner in WENZ, 1940, for the superfamily Tryblidioidea. It was intended to be of the same rank as Polyplacophora and conceived to contrast the Polyplacophora. This stabilizes the name as the name of the class containing *Tryblidium*

Lindström, 1880, and its type species *T. reticulatum* Lindström, 1880. The name Monoplacophora has since been extensively used to include Tryblidioidea (*sensu* Wenz) as the most important taxon. Later some authors have added and removed smaller groups of Paleozoic mollusks. We do not consider such changes in the concept of a taxon to be a convincing reason for changing its name. We have not noticed that the proponents for abandonment have suggested changing the name Gastropoda, another class that has been exposed to similar transfers of Paleozoic taxa.

The following abbreviations for institutions are used in the text: SMF—Senckenbergisches Museum und Forschungsinstitut, Frankfurt; SMNH—Swedish Museum of Natural History, Stockholm.

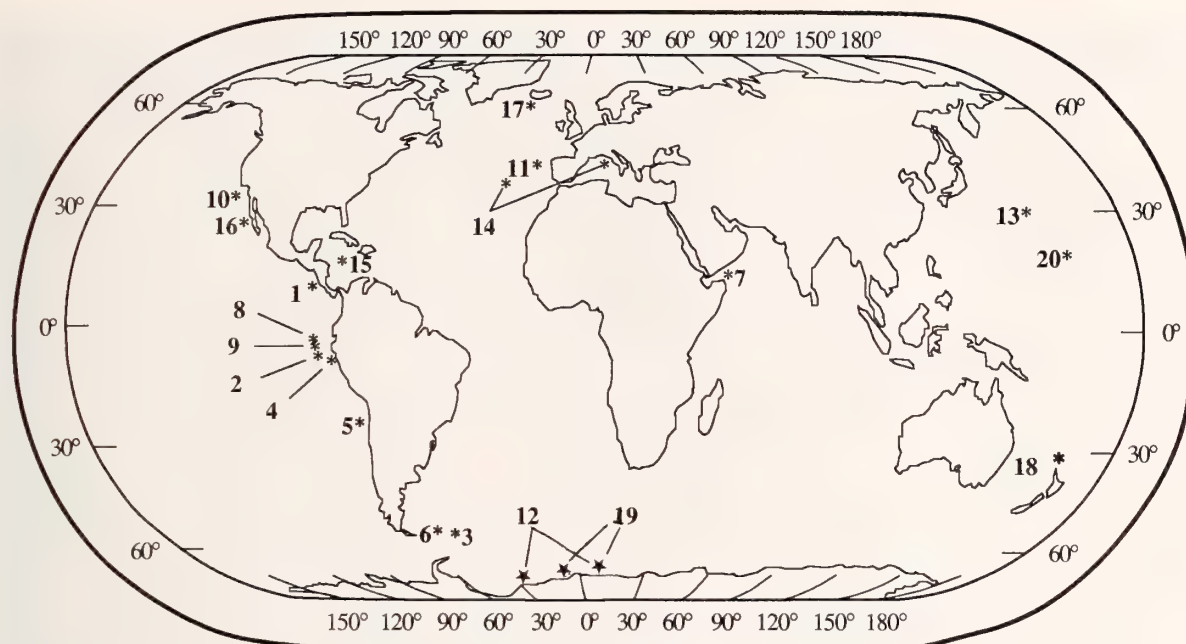


Figure 1

Map showing distribution of Recent Monoplacophora, based on Table 1.

Laevipilina McLean, 1979

Vema (*Laevipilina*) McLEAN 1979:9. Type species, *V. (L.) hyalina* McLean, 1979, by original designation. Type locality, off Lower California, 373–384 m.

Remarks: MOSKALEV *et al.* (1983) considered *Laevipilina* to be a valid genus and made a new family for it. WARÉN (1989) considered *Monoplacophorus* Moskalev, 1983 (type species *M. zenkewitchi* Moskalev *et al.*, 1983) to be a synonym of *Laevipilina*, but has since changed his opinion; *Monoplacophorus* can probably be considered a valid genus, differing from *Laevipilina* by its more depressed shape. WARÉN & BOUCHET (1990) reviewed current knowledge about *Laevipilina* and described *Laevipilina rolani*, a new species from off northwestern Spain in 1000 m depth.

Laevipilina antarctica Warén & Hain, sp. nov.

(Figures 2–5, 6–8, 10–14, 15–16, 19, 27)

Type material: Holotype (Figure 3), SMF 309243, and 2 broken paratypes (radula extracted) SMF 309244; 4 paratypes (1 sectioned) from station 248, SMNH 4285, 1 from station 158, SMNH 4352.

Type locality: *Polarstern* Expedition ANT VII/4, station 245, 75°40.4'S, 029°37.2'W, 480 m, 3 specimens. Sand and gravel with stones and rich megafauna (see ARNTZ *et al.*, 1990).

Materials examined: The type material and:

—*Polarstern* Expedition ANT VII/4, station 248,

74°39.3'S, 029°34.4'W, 600 m, sand and gravel with stones and rich megafauna (see ARNTZ *et al.*, 1990), 4 specimens (1 specimen serially sectioned, 3 specimens left in alcohol).

—*Polarstern* ANT IX/3, station 158, 72°21.8'S, 16°51.2'W to 72°21.0'S, 16°48.6'W (end of haul), 623–539 m, 1 specimen, 1.26 mm diameter, on a stone of 15 cm diameter.

—*Polarstern* ANT IX/3, station 174, 69°43.7'S, 10°44.7'E to 69°42.4'S, 10°47.5'E, 432–432 m, silt with small stones, 1 specimen, 1 shell.

—*Polarstern* ANT IX/3, station 180, 69°57.4'S, 06°19.0'E to 69°57.7'S, 06°21.0'E, 280–298 m, 1 specimen, 2.4 mm diameter.

—*Polarstern* ANT IX/3, station 207, 69°57.4'S, 05°08.4'E to 69°57.5'S, 05°00.4'E, 213–210 m, silt with scattered stones with rich megafauna, large quantities of the brachiopod *Magellania fragilis* Smith, 1907, 1 specimen, 2 shells.

—*Polarstern* ANT IX/3, station 212, 70°00.5'S, 03°56.4'E to 70°00.4'S, 03°57.3'E (end of haul), 568–644 m, 1 specimen, 3.0 mm diameter, on a boulder of 80 cm diameter, 4 specimens and 1 shell free in sediment.

Description: The shell (Figures 2–5) is small, fragile, depressed, and transparent with a flat peristome. The apex (Figure 2) is slightly mamillate, forms an angle of about 60° with the basal plane, and is situated slightly behind the anterior margin. The apical area measures 230 × 190 µm and has no distinct sculpture, only some regularly shaped impressions. Outside this area commences a uniform, concentric sculpture of low, raised ridges, formed by the concentric arrangement of the prisms of the prismatic



Explanation of Figures 2 to 5

Figures 2-5. *Laevipilina antarctica* Warén & Hain, sp. nov., shell.

Figure 2. Lateral view of apex. Scale line 50 μ m. *Polarstern* station 158.

Figure 3. Dorsal view of holotype, periostracum removed. Length 2.06 mm.

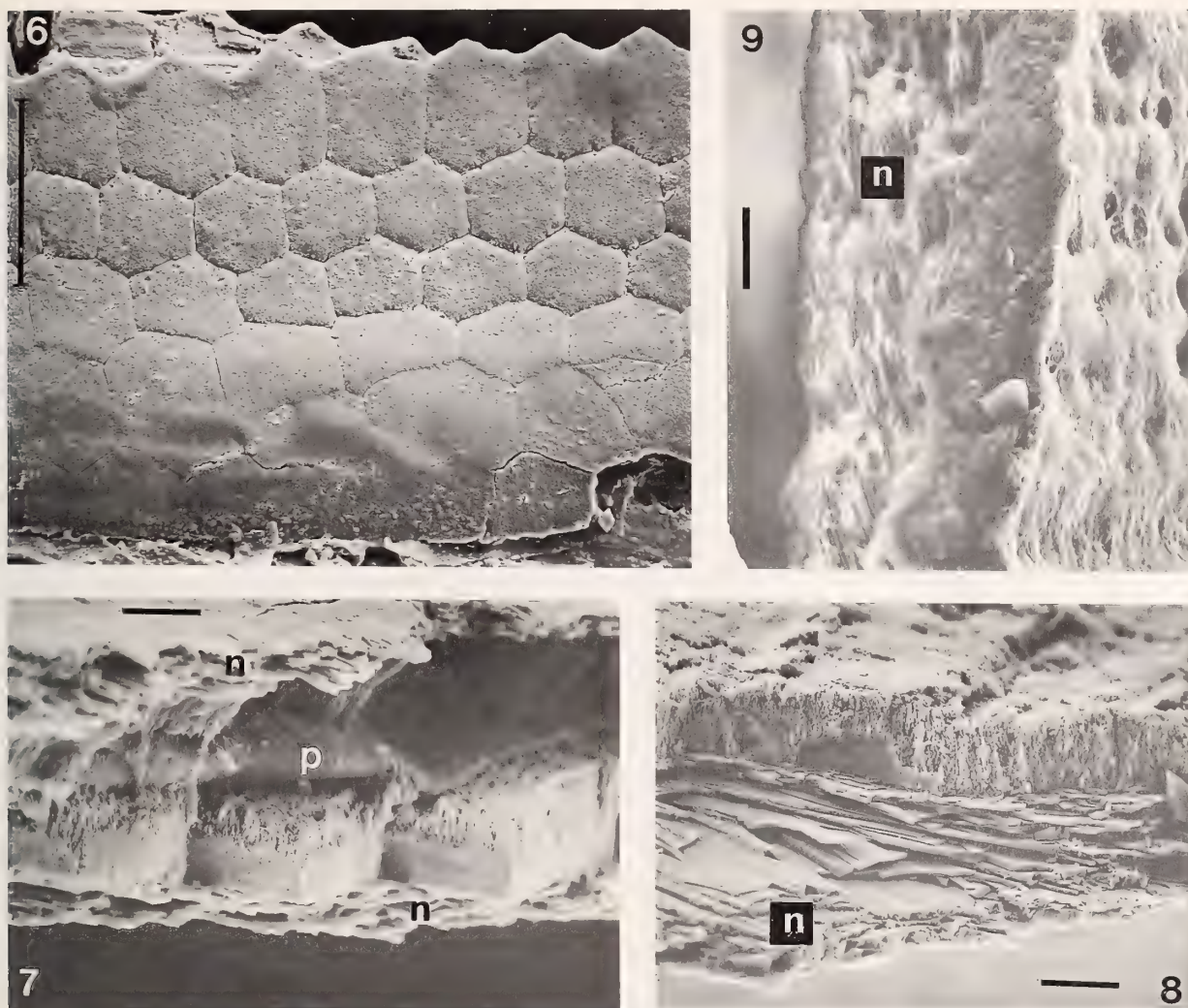
Figures 4 and 5. Dorsal and lateral view, periostracum left. Length 1.26 mm. *Polarstern* station 158.

layer, which also form indistinct and fragmentary radial ridges. The shell is rather low, with the posterior surface evenly convex and the highest point situated somewhat behind the apex. The prisms (Figures 6-8) are regularly hexagonal and have a diameter of about 30 μ m and a height of about 15 μ m. Towards the edge of the shell they are larger and less uniformly shaped (Figure 6). The thickness of the nacreous layer (Figures 7, 8) is 5-10 μ m, and

it starts only a short distance from the margin of the shell. The periostracum is rather thick and tough.

Dimensions. Holotype, length 2.06, breadth 1.76, and height of shell 0.50 mm. Maximum length of the shell 3.0 mm.

Soft parts (Figures 15, 16, 19). The velar lobes are well developed and strongly ciliated. The anterior lip is conspicuous and evidently rather thinly cuticularized. The



Explanation of Figures 6 to 9

Figures 6–8. *Laevipilina antarctica*, shell structure.

Figure 6. Interior view of edge of shell (facing lower edge of figure). Scale line 50 μm . Figure 7. Fragment of shell, folded double and held together by the periostracum (p). Prismatic layer partly dissolved between periostracum and nacre (n). Scale line 10 μm . Figure 8. Fragment of shell, prismatic layer (p) partly dissolved, nacreous (n) layer intact. Scale line 10 μm .

Figure 9. *Micropilina arntzi* Warén & Hain, sp. nov., shell structure. Fragment of shell, exterior surface facing right. Nacreous layer (n) well developed. Scale line 10 μm .

postoral tentacles are much less developed compared with *Laevipilina rolani*, and are more similar to those in *L. hyalina*. They are short and claviform and equipped with about 7 short and stumpy distal appendages. The gills are not well preserved, but the smallest specimen (1.1 mm) has four pairs of gills with 0 (anterior pair), 0, 1, and 1 (posterior pair) "digits," respectively. The largest specimen (from station 212; Figure 19) is well preserved. It has 3, 4, 4, 4, and 4 digits, respectively, on the gills starting with the anterior one. The foot (contracted) measures 1.5

\times 0.9 mm. The gonads are visible, by transmitted light, as a large, lobate, dorsal sac along each side of the animal. The anus does not open on a papilla, but is a simple opening in the pallial furrow. The four coils of the intestine could not be discerned by transmitted light.

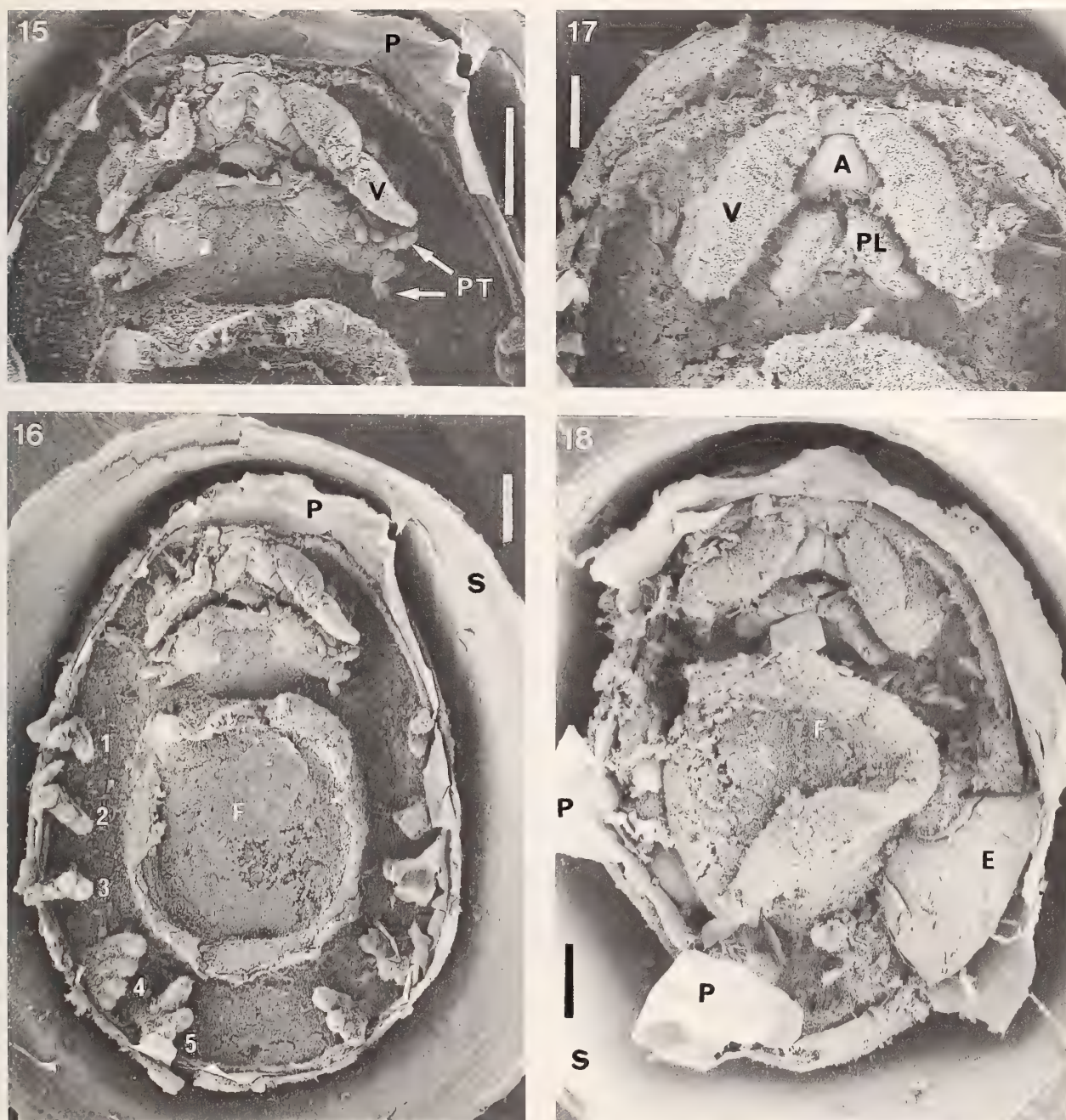
Radula (from a 1.5 mm specimen; Figures 10–14, 27). Length 1.6 mm, width 0.066 mm, with about 65 transverse rows, each of 11 teeth. The outermost tooth (assigned number 6) has no distinct cusp, and an only slightly uneven cutting edge. Tooth number 5 is large, fan-shaped, and



Explanation of Figures 10 to 14

Figures 10–14. *Laevipilina antarctica*, radula. Figure 10. Posterior view. Figure 11. Anterior view. Figure 12. Vertical view. Figure 13. Detail of central tooth, posterior view. Figure 14. Newly formed section of radula. Notice the incompletely formed fourth and fifth tooth.

Numbers indicate the order of the teeth; the central tooth is 1. Scale lines are 10 μm except Figure 13, which is 5 μm .

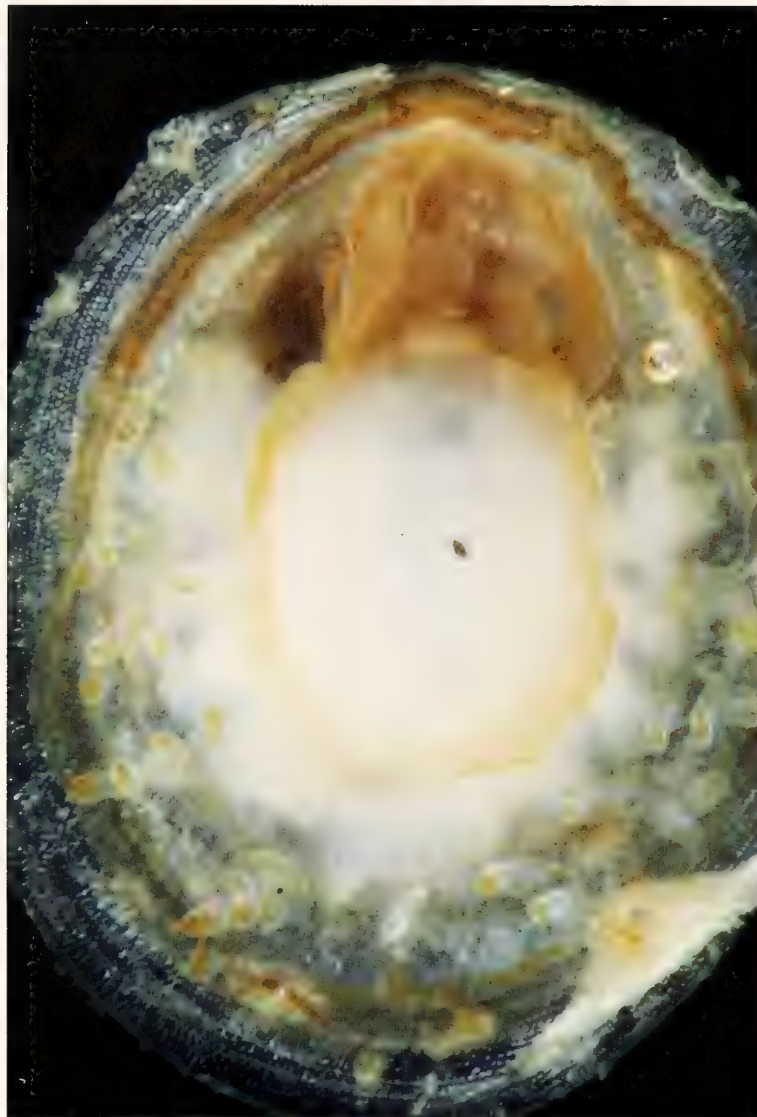


Explanation of Figures 15 to 18

Figures 15 and 16. *Laevipilina antarctica*. Critical point dried bodies. Scale lines 200 μ m. *Polarstern* station 173.

Figures 17 and 18. *Micropilina arntzi*. Critical point dried bodies. Fragments of the periostracum are still attached to the pallial margin and the shell. Scale lines 100 μ m. *Polarstern* station 173.

Key: A, anterior lip; E, embryo; F, foot; P, periostracum (pulled off from shell); PL, posterior lip; PT, postoral tentacles; S, shell; V, velum; 1-5, gills in numerical order.



Explanation of Figure 19

Figure 19. *Laevipilina antarctica*, living specimen, diameter 3.0 mm. *Polarstern* station 212.

somewhat similar to a hay-rake, with about 50 lamellar hooks. Tooth number 4 has a truncated and serrated cutting edge. Tooth number 3 is slightly smaller than number 4 and has a laterally situated main cusp and about 6 or 7 more central denticles. Tooth number 2 is hand-shaped, with two apically and laterally situated primary cusps and some smaller denticles along the inner side. The central tooth is small, inconspicuous, ridgelike with a small apical cusp.

The large and conspicuous tooth number 5 is the last one to be formed during the continuous process of radular formation (Figure 14).

Remarks: The prismatic layer is barely visible in incident light, while the concentric sculpture dominates. In transmitted light the prisms are clearly visible (Figure 19).

The apical area (Figure 2) is probably a larval shell, as is indicated by the presence of a periostracum of which only patches remain. The periostracum was evidently continuous and covered all the shell, but a part of it still covers the transition from the apical area, over to the part of the shell that has concentric and radial sculpture.

Laevipilina antarctica differs from *L. hyalina* in having a less prominent central radular tooth and in having five instead of six pairs of gills, although the specimens are of

the same size. Another difference is that the prisms of *L. hyalina* are about as high as they are wide, while in *L. antarctica* they are distinctly shorter than they are wide. *Laevipilina rolani* differs in having more fully developed postoral tentacles, and in having a more convex shell, its height corresponding to half the length of the shell, while it is only 0.33 of the length in *L. antarctica*.

The specific identification of monoplacophorans is still a problem since very few species are known from more than a single locality and several of the species belonging to genera of small species are very similar to each other. We are therefore not certain about the validity of the criteria used for their separation. It is even possible that *Laevipilina antarctica* belongs to one of the previously described species, although experience from gastropod limpets suggests otherwise.

In this connection it is significant to note that the number of digits on the gills varies with the size of the specimens, as mentioned in the description of the soft parts. The postoral tentacles, however, are identical throughout ontogenetic development, as far as could be seen.

Most specimens were found free in sediment samples brought home and sorted in the laboratory; only two specimens (from stations 158 and 212) were found on stones after intensive search of hundreds of stones of various sizes. This may be because they are scratched off the stones or crushed in the trawl by the surrounding bottom material. We therefore assume that all specimens had been living on stones or old shells, which were common in the bottom material of all stations.

One small specimen was serially sectioned to examine the stomach contents, which consisted of numerous mineral particles, unidentified organic material, scattered sponge spicules, radiolarian fragments, a small nematode, and a few polychete bristles.

The end of the radula that is in use shows conspicuous signs of wear. Most of the cusps of teeth numbers 1–4 are worn off to form a simple, rounded edge (Figure 27) instead of a sharp serration. This supports the assumption that *Laevipilina antarctica* obtains its food by scraping off the thin layer of sediment, which in these depths covers most hard surfaces.

Micropilina Warén, 1989

Micropilina WARÉN, 1989:2. Type species, *M. minuta* Warén, 1989, by original designation. Type locality, off southwestern Iceland, 900–926 m.

Remarks: The genus was based on a few empty shells, characterized by the shape, sculpture, and presence of distinct interior muscle scars. MARSHALL (1990) described a second species of the genus from north of New Zealand (Figure 1, number 18), from 1216–1385 m depth, known from a single shell.

The new species described here conforms well with a

position in *Micropilina*. The shape is similar to that of the previously described species, and the sculpture is of the same construction, although finer.

The sculpture of the species of *Micropilina* bears some resemblance to that of the subapical part of the shell of *Rokopella* (WARÉN, 1988:figs. 3, 8), but it is too early to judge what this means about relationships, since the shell of most monoplacophorans has not been well enough illustrated to allow comparisons.

Micropilina arntzi Warén & Hain, sp. nov.

(Figures 9, 17, 18, 20–26, 28, 29)

Type material: Holotype SMF 309780 and 5 paratypes SMF 309781, 20 paratypes SMNH 4380.

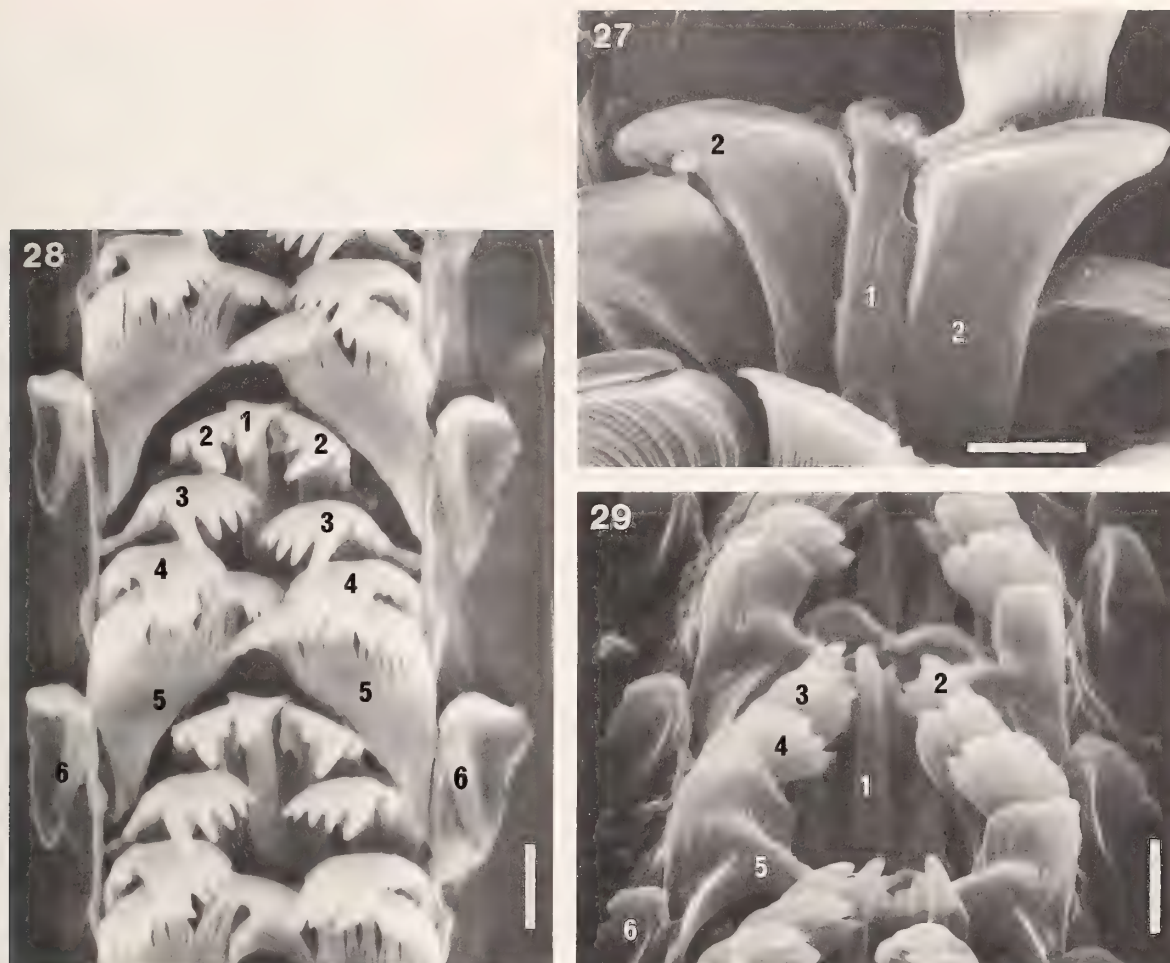
Type locality: R/V *Polarstern* ANT IX/3, station 173, 70°00.5'S, 07°09.1'E to 70°00.4'S, 07°07.4'E (end of haul), 739–765 m, 25 specimens, 10 shells, maximum diameter 0.92 mm.

Material examined: The type material and:

- Polarstern* ANT IX/3, station 165, 70°18.9'S, 03°15.8'W to 70°19.2'S, 03°16.8'W, 191–204 m, silt with stones and rich megafauna, 1 shell, 1 specimen.
- Polarstern* ANT IX/3, station 174, 69°43.7'S, 10°44.7'E to 69°42.4'S, 10°47.5'E, 432–432 m, silt with small stones, 7 specimens, 15 shells, maximum diameter 0.85 mm.
- Polarstern* ANT IX/3, station 180, 69°57.4'S, 06°19.0'E to 69°57.7'S, 06°21.0'E, 280–298 m, 17 specimens, 1 shell, maximum diameter 0.88 mm.
- Polarstern* ANT IX/3, station 206, 69°06.9'S, 10°01.0'E to 69°46.8'S, 10°01.6'E, 343–338 m, 1 shell.
- Polarstern* ANT IX/3, station 207, 69°57.4'S, 05°08.4'E to 69°57.5'S, 05°00.4'E, 213–210 m, silt with scattered stones with rich megafauna, large quantities of the brachiopod *Magellania fragilis* Smith, 1907, 2 shells, 1 specimen.
- Polarstern* ANT IX/3, station 211, 69°58.9'S, 05°08.4'E to 69°57.9'S, 05°00.4'E, 661–742 m, 5 shells.
- Polarstern* ANT IX/3, station 212, 70°00.5'S, 03°56.4'E to 70°00.4'S, 03°57.3'E, 568–644 m, 4 specimens.

Descriptions: The shell (Figures 20–26) is very small, fragile, inflated, almost semiglobular with a large, bulbous apex and flat peristome. The apex (Figure 24) is mamillate and forms an angle of about 45° with the basal plane (Figure 22). There is no distinct sculpture on the slightly worn apical area, apart from occasional small pits, which also were seen in late, brooded young. This area measures 300 × 270 µm. Outside this area commences a fine, irregularly concentric striation (Figure 25), not visible with a stereomicroscope. In the furrows between the ridges are numerous small pits, diameter 2–5 µm. Under a stereomicroscope the whole shell has a seemingly granular surface, but this is caused by the pits. The shell is unusually





Explanation of Figures 27 to 29

Figure 27. *Laevipilina antarctica*, central part of radula with worn edges of teeth number 1 and 2.

Figures 28 and 29. *Micropilina arntzi*, radula, in perpendicular view and with stub tilted 45° to show the posterior surface of the cusps.

Teeth numbered 1–6 from central tooth (1). Scale lines 5 μm .

convex, with the apex well in front of the anterior edge and the highest point of the shell slightly anterior to the center of the shell. No muscle scars could be discerned on the interior. Slightly more than half the thickness of the shell consists of an interior nacreous layer (Figure 9), the exterior layer does not contain defined prisms.

Dimensions. Holotype 0.84 \times 0.76 mm, height 0.38 mm. Maximum length of the shell 0.92 mm.

Soft parts (Figures 16, 18). The head is unusually large and bulging, with short, tapering, strongly ciliated velar lappets at the sides. The anterior lip seems to be very solid and cuticularized. Postoral tentacles are not present. The

Explanation of Figures 20 to 26

Figures 20–26. *Micropilina arntzi*, shell. Figure 20. Fully developed juvenile from oviduct. Length 305 μm . *Polarstern* station 173. Figures 21–24. Anterior view, lateral view, dorsal view, and apex magnified. Length 0.92 mm. Scale line (Figure 24, only) 50 μm . *Polarstern* station 173. Figures 25 and 26. Dorsal view and sculpture. Length 0.85 mm. Scale line (Figure 25 only) 50 μm . *Polarstern* station 211.

White arrows indicate border of larval shell.

foot is round with a thickened rim. Three pairs of small, simple, tubercular gills are situated in the pallial groove and lack appendages. Five small, close-set muscle bundles, diameter 20–50 μm , can be seen with transmitted light, situated along the central third of the body and halfway between the midline and the lateral margin. Most specimens have one or two embryos under development, evidently partly contained in the opening of the gonoduct. The smallest embryos were ovate and of a diameter of about 100 μm , the largest ones 300 μm (Figure 20).

Radula (Figures 28, 29). The length of the radula slightly exceeds that of the shell. The outermost tooth (number 6) is scalelike with a smooth, rounded cutting edge. The large tooth (number 5) has about 20 or 25 hooks in the rake-like comb of teeth. Teeth numbers 4, 3, and 2 resemble each other and have 7, 6, and 4 cusps, respectively. The size of these three teeth diminishes towards the center of the ribbon. The central tooth (number 1) has a fully formed, tricuspidate cutting plate and a sturdy, narrow central supporting ridge.

Remarks: Among the monoplacophorans described so far, this one has been found in the greatest numbers, and it is the only one for which the mode of development is known. The young are evidently born at the crawling stage.

The increase in size of the embryos must mean that some kind of transfer of nutrients, supplied by the parent, takes place, but the mechanism is not known.

The radula of *Micropilina arntzi* is unusual in that the central and first marginal teeth are less reduced than in all other species for which the radula has been described. Those species have a radula that more closely resembles those of *Laevipilina* species.

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Drs. B. A. Marshall (Wellington) and J. H. McLean (Los Angeles) read and gave valuable comments on the manuscript.

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Comments on and Descriptions of Eulimid Gastropods from Tropical West America

by

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Abstract. The author and date of the family name Eulimidae is corrected from H. & A. Adams, 1853, to Philippi, 1853, on the basis of priority. *Turveria pallida* sp. nov. is described from the Gulf of California. It is ectoparasitic on the sand dollar *Encope grandis* L. Agassiz, 1841. *Microeulima* gen. nov. is described with the type species *Alaba terebralis* Carpenter, 1857 (*Eulima proca* de Folin, 1867 = *Leiostraca schwengela* Bartsch, 1938 = *Strombiformis hemphilli* Bartsch, 1917 [new synonyms]). This species occurs from northern Mexico to Ecuador in shallow water. *Strombiformis hemphilli* Dall, 1883, from Florida, is placed in *Microeulima*. *Scalenostoma babylonica* Bartsch, 1917, is a junior synonym of *Chemnitzia rangi* de Folin, 1867, which is transferred from *Scalenostoma* to *Niso* Risso, 1826. *Eulimostraca* Bartsch, 1917 is discussed and *E. macleani* sp. nov. is described from Costa Rica. *Strombiformis burraei* Bartsch, 1917 (= *Melanella panamensis* Bartsch, 1917 [new synonym]) and *Leiostraca linearis* Carpenter, 1857, are transferred to *Eulimostraca* (all from western Mexico and Central America). *Eulimetta pagoda* gen. et sp. nov. is described from western Central America. Its host species is unknown. *Sabinella shaskyi* sp. nov. is described from western Central America. It lives in galls in the spines of the cidaroid sea urchin *Eucidaris thourarsi* (Valenciennes, 1846).

INTRODUCTION

The family Eulimidae contains a large number of species, almost exclusively parasitic on echinoderms. The shell morphology is highly diverse and there are, in addition to species of “typical eulimid” appearance, also limpets and shell-less species in the family (WARÉN, 1984b).

To some extent the development of the shell depends on the animal's sex or on the presence or absence of additional individuals of the same species, which in some species determine the sex of newly settled larvae (WARÉN, 1984b). This complicates specific classification, but the problem can be overcome by a comparison of larval shells, which are identical within a species.

This paper presents some of the results of an examination of the West American eulimid collections in the Los Angeles County Museum of Natural History and the U.S. National Museum of Natural History, made some 15 years ago. During the intervening years I had hoped to obtain further material of the species discussed here, to be able to describe them in more detail and consolidate their systematic position. This has failed, however, except for the new species of *Turveria* and *Sabinella*. Nevertheless, I describe them here in an attempt to draw the attention of workers to them.

When looking for eulimids, it is always useful to examine echinoderms, which are usually their hosts. This can easily be done by selecting a common echinoderm species and, after a brief examination of each specimen, shaking them in a bucket with brackish water or seawater with some cleansing substance added (e.g., formalin or detergent). Afterwards the residue on the bottom of the bucket is searched for specimens. If any are found, they should be saved together with at least one specimen of the host. This procedure is quite profitable, and frequently yields undescribed species, in addition to invaluable information about species already known.

Abbreviations and Conventions Used in Text

BMNH—Natural History Museum, London.

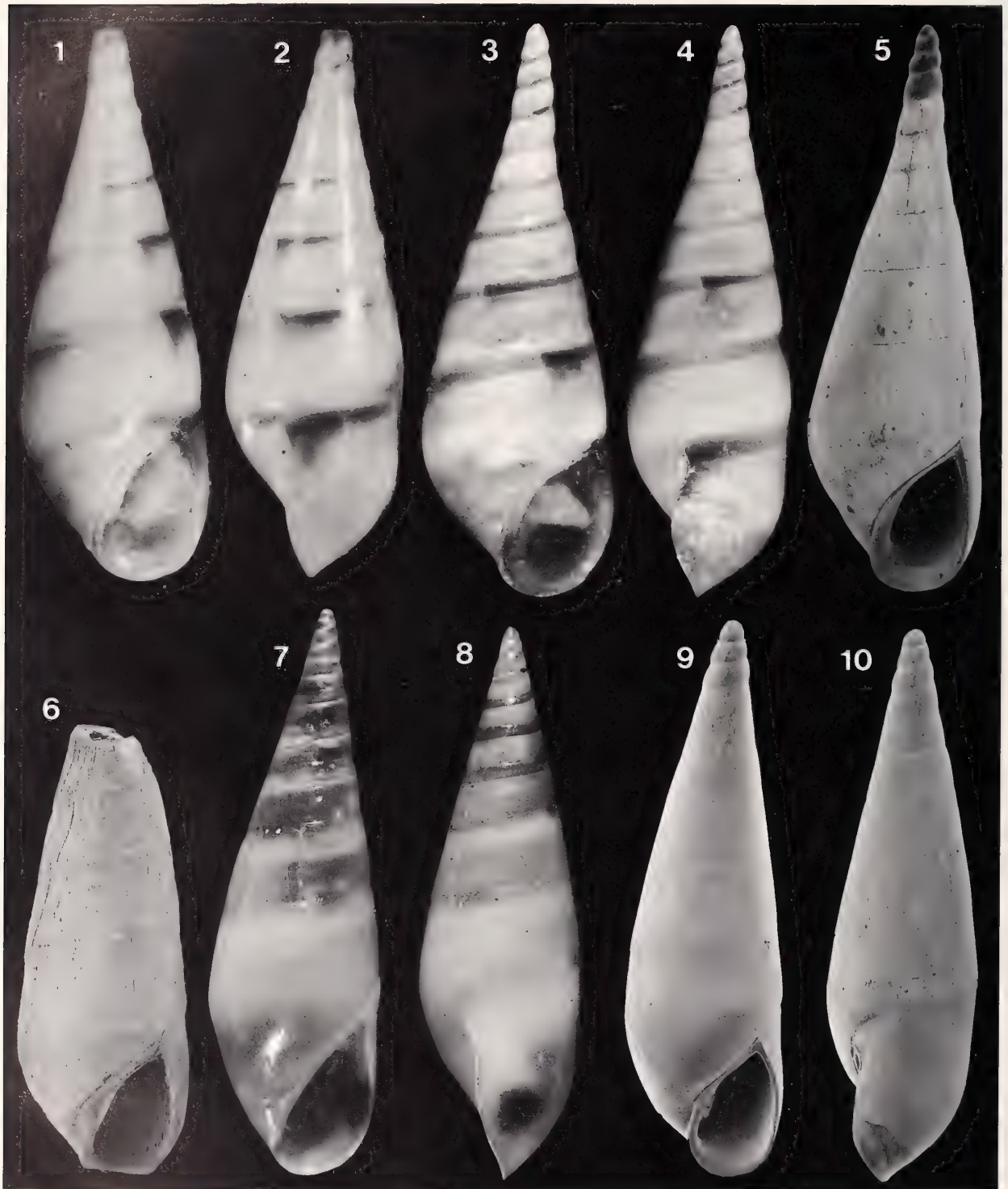
LACM—Los Angeles County Museum of Natural History, Los Angeles, California.

SMNH—Swedish Museum of Natural History, Stockholm.

USFC—United States Fish Commission.

USNM—National Museum of Natural History, Washington, D.C.

In the enumerations of examined material, “shell” is



Explanation of Figures 1 to 10

Figures 1 and 2. *Microeulima terebralis*, holotype of *Leiostraca schwengelae*, USNM 127554, 3.12 mm.

Figures 3 and 4. *Microeulima terebralis*, Costa Rica, LACM 72-46.16, front view (2.80 mm) and side view (3.28 mm).

Figure 5. *Microeulima terebralis*, Costa Rica, LACM 72-42.20, front view 2.94 mm.

used for empty shells, whereas "specimen" is used for shells containing dried or preserved soft parts.

SYSTEMATICS

Family EULIMIDAE Philippi, 1853

The family name has usually been ascribed to H. & A. ADAMS (1853:235) (WARÉN, 1984b; PONDER & WARÉN, 1988). The name was published by the Adams brothers in the eighth section of their monograph, which was issued December 1853. This is later than the publication by PHILIPPI (1853:194), which was published before May 1853, since Philippi's book was reviewed by PETIT (1853) in the May issue of the *Journal de Conchyliologie*. The correct author of the family is thus Philippi, 1853.

Turveria Berry, 1956

Turveria BERRY, 1956:356. Type species, by original designation, *Turveria encopendema* Berry, 1956, Mexico, Baja California Sur, on sand dollars, *Encope* spp. (Scutellidae).

Remarks: The genus was redescribed by WARÉN (1991), and two species parasitic on sand dollars in the Gulf of California were included. The second species was wrongly identified as *Turveria schwengelae* Bartsch, 1938, a mistake which is corrected below.

Little is known about the biology of the species of *Turveria*, except that they are regularly found on specimens of sand dollars belonging to the genus *Encope* L. Agassiz, 1841, a genus endemic to the southeastern United States, the Caribbean, Galapagos, and the American west coast from California to Ecuador (MORTENSEN, 1948).

Turveria pallida Warén, sp. nov.

(Figures 7, 8, 13)

Turveria schwengelae: WARÉN 1991:108, figs. 10A, B, 13F, G (not Bartsch, 1938).

Type material: Holotype LACM 2425 (from LACM 55554) and 2 paratypes LACM 2426 (from LACM 55553), 2 paratypes SMNH 4122 (from LACM 55554; for locality data see "Material examined"). Further paratypes, 12 specimens SMNH 4141 and numerous specimens in D. Shasky collection, from the same locality.

Type locality: Mexico, Baja California Norte, sand flats at Isla Willard, Bahia San Luis Gonzaga, 29°57'N, 114°17'W, on *Encope grandis*, 3 specimens, LACM 55554.

Material examined: The type material and MEXICO: Baja California Sur, Bahia Concepcion, 26°42'N, 115°55'W, 1 shell, no host (LACM 63-37.3); Baja California Norte, Isla Willard, Bahia San Luis Gonzaga, 29°57'N, 114°17'W, on *Encope* sp., 4 specimens (LACM 55553 [paratypes LACM 2426 and SMNH 4122]); Baja California Norte, Bahia San Luis Gonzaga, 29°57'N, 114°17'W, on *Encope grandis*, intertidal, 36 specimens (D. Shasky collection [12 specimens paratypes SMNH 4141]).

Description: (Sex not known.) The shell (Figures 7, 8) is conically lanceolate, solid, smooth, transparent, with brownish markings along the suture and on the outer lip. The larval shell (Figure 13) consists of about 2.7 distinctly convex whorls and is smooth and colorless except for an occasional brownish tint on the initial whorl. The visible height of the larval shell is 260 μ m, and the total height of the shell of the larva is estimated to about 290 μ m. The holotype has 7.25 teleoconch whorls of slowly and uniformly increasing diameter, sculptured by numerous dense and sharp incremental lines. The teleoconch of the holotype has nine incremental scars (1.2, 1.9, 2.8, 3.8, 4.3, 4.8, 5.5, 6.0, and 6.6 whorls from the outer lip) but as usual there is some individual variation in this character. The suture is shallow but distinct and makes a conspicuous bend downwards about 0.3 mm before the outer lip. The aperture is constricted in its upper part as a consequence of this and is pear-shaped. The outer lip is distinctly prosocline, with a shallow sinus below the suture. The color pattern is not as bright as in *Turveria encopendema*, and consists of a brownish spiral band just below the periphery of the body whorl. This band is concealed under, or visible through, the subsutural zone on earlier whorls. There is also a large, roundedly triangular blotch at the lower part of the outer lip and one less-distinct, sometimes absent, similar spot just below the corner between the outer lip and the suture.

Dimensions. Height of holotype 5.23 mm, maximum height 5.8 mm.

Remarks: *Turveria pallida* differs from *T. encopendema* by having a regularly conical spire, flatter whorls, and less vivid color pattern, and by being about $\frac{1}{2}$ taller (shell height 4.91 ± 0.27 mm [SD] among 23 mature specimens; compared with 4.18 ± 0.27 mm among 26 specimens of *T. encopendema*).

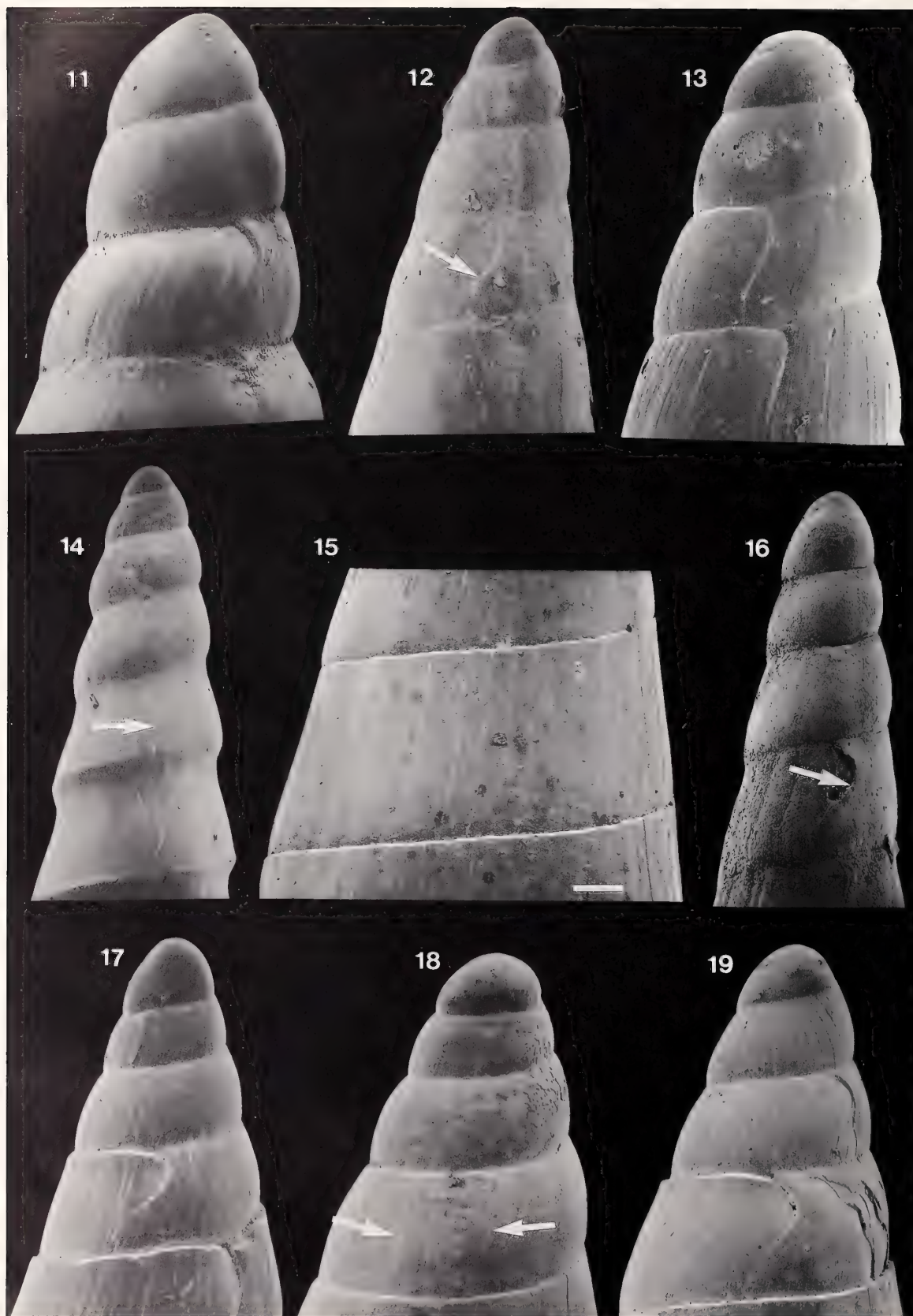
Eulima Risso, 1826

Eulima RISSO, 1826:123, type species pending (WARÉN, 1992), suggested to be *Strombiformis glaber* Da Costa, 1778, European.

Figure 6. *Microeulima* sp. from the sea urchin *Chaetodiadema granulatum*, northwest of Koh-si-Chang, Thailand, 18 m depth, height 3 mm. Zoological Museum of the University of Copenhagen.

Figures 7 and 8. *Turveria pallida*, paratypes, LACM 2426, side view 4.88 mm and front view 4.96 mm.

Figures 9 and 10. *Microeulima hemphilli*, Florida, syntype, USNM 35983, height 3.1 mm.



Remarks: The genus *Eulima* was described anatomically by WARÉN (1984a). The hosts are known for two European species, in both cases ophiuroids (WARÉN, 1984a, and unpublished data). Almost all species that at present can be classified in *Eulima* still remain unknown with respect to anatomy and host choice.

The species of *Eulima* s.s. have a tall (7–20 mm), slender shell, usually with a brownish color pattern, flat whorls, and a tall aperture with a rather straight profile of the outer lip. The animal is not very modified anatomically and retains a small stomach and a buccal mass with a ptenoglossate radula. The type species is a sand dweller, parasitic on ophiuroids, and has large epipodial folds, partly covering the base of the shell in order to facilitate the movements in the sand.

The generic name *Strombiformis* Da Costa, 1778, has been used extensively in American literature, but the type species is an European pulmonate (WARÉN, 1984b).

BARTSCH (1917) revised the western American eulimids and classified several species in *Strombiformis*. Of the West American species the following seem to belong to *Eulima* s.s., judging from shell characters: *S. almo* Bartsch, 1917; *S. barthelowi* Bartsch, 1917; *S. californica* Bartsch, 1917; *Eulima fuscostrigata* Carpenter, 1864; *S. lapazana* Bartsch, 1917; *S. panamensis* Bartsch, 1917; *Eulima recta* C. B. Adams, 1852; *S. townsendi* Bartsch, 1917; and *E. varians* Sowerby, 1834. BARTSCH (1926) also described *Strombiformis hua*, *S. salsa*, *S. inca*, and *S. paria*, all of which belong to *Eulima* s.s. Not all of these names represent different species, but I am not prepared to present a detailed synonymy.

A large proportion of all the species of Eulimidae were originally described in *Eulima*, and are still placed there. Therefore I have frequently placed species provisionally in *Eulima*, instead of describing new genera for them.

Microeulima Warén, gen. nov.

Type species: *Alaba terebralis* Carpenter, 1857, western Central America.

Diagnosis: Small eulimids, 2.5–5 mm high, with a slender, lanceolate shell of slowly increasing diameter, flat whorls, and brownish color, either as sutural and collabral bands or uniformly all over shell. Fine, sharp, indistinct axial lines present. Aperture constricted in its right corner, evenly and broadly rounded at opposite end. Outer lip with distinct subsutural sinus. Parietal callus thick and abruptly demarcated.

Etymology: *Microeulima*, from Greek *mikros*, meaning “small,” and *Eulima*, referring to the similarity to species of *Eulima* s.s.

Remarks: I hesitated much before describing this new genus since there is neither a species of which soft parts have been examined, nor a named species for which the host is known. The group of species I classify here is, however, well demarcated, and there are numerous species in tropical areas, almost all of them undescribed.

The host is known for a single species, but the shell is in such bad condition that it cannot be described or specifically identified, although the aperture indicates that it belongs to *Microeulima*. This species was found by T. Mortensen (unpublished data) parasitizing the diadematid sea urchin *Chaetodiadema granulatum* Mortensen, 1903, in Thailand, northwest of Koh-si-Chang, in 18 m depth. The shell (Figure 6) has a broken apex and the surface is corroded, but the soft parts remain.

In this genus belongs *Strombiformis hemphilli* (Dall, 1883) which was described from Cedar Keys, Levy County, Florida, and later (LYONS 1989:16) recorded from several localities at Hutchinson Island, off Indian River, St. Lucie County, eastern Florida. I figure one of the two syntypes (Figures 9, 10). The shell of this species is uniformly chestnut brown.

The genus *Eulimostraca* (see below) bears some resemblance to *Microeulima*, but the shape of the shell is regularly conical with a larger aperture and it lacks the axial lines typical for *Microeulima*.

Microeulima also resembles *Turveria*, but species of that genus lack the strongly developed parietal callus.

←

Explanation of Figures 11 to 19

Figure 11. *Eulimostraca macleani*, paratype, LACM 2371, height of larval shell 390 μ m.

Figure 12. *Eulimostraca galapagensis*, paratype, USNM 251281, height of larval shell 400 μ m.

Figure 13. *Turveria pallida*, paratype, LACM 2426, height of larval shell 260 μ m.

Figure 14. *Eulimetta pagoda*, holotype, LACM 2372, height of larval shell 210 μ m.

Figure 15. *Niso interrupta*, Mexico, near Guaymas, Bahia Bacochibampo, 9–18 m, LACM 55558. Scale line 0.25 mm.

Figure 16. *Microeulima terebralis*, Costa Rica, LACM 72-42.20, height of larval shell 490 μ m.

Figure 17. *Niso rangi*, Costa Rica, LACM 72-52.22, height of larval shell 370 μ m.

Figure 18. *Niso interrupta*, LACM 55558, for collection data see Figure 15, height of larval shell 490 μ m. Left arrow indicates a teleoconch growth line, right arrow a protoconch growth line.

Figure 19. *Niso hipolitensis*, Mexico. Baja California Sur, Punta Palmilla, intertidal, LACM 66-11.5, height of larval shell 390 μ m.

Eulimostroma bartschi Strong & Hertlein, 1937, known from two localities in western Mexico (HERTZ & HERTZ, 1982), probably belongs to *Microeulima*, but I have not examined any specimens.

***Microeulima terebralis* (Carpenter, 1857)**

(Figures 1–5, 16)

Alaba terebralis CARPENTER, 1857:367.

Leiostraca sp. ind. (b): CARPENTER 1857:440.

Eulima proca DE FOLIN, 1867:62, pl. 6, fig. 3 (new synonym).

Strombiformis hemphilli BARTSCH, 1917:344, pl. 47, fig. 4 (not Dall, 1889) (new synonym).

Leiostraca schwengelae BARTSCH, 1938:34 (replacement name for *Strombiformis hemphilli* Bartsch, 1917).

Alaba terebralis: BRANN 1966:pl. 40, fig. 427.

Leiostraca sp. ind. (b): BRANN 1966:pl. 40, fig. 553.

Eulima? *terebralis*: KEEN 1968:424, text fig. 108.

Type materials: *Alaba terebralis*, holotype BMNH 1854.6.4.427; *E. proca*, 1 syntype BMNH 1868.2.17.13; *S. hemphilli*, holotype USNM 127554 (Figures 1, 2).

Type localities: *Alaba terebralis*, W Mexico, Sinaba, Mazatlan, “off *Spondylus*” (living on?); *E. proca*, Panama, Archipelago de las Perlas; *S. hemphilli*, Baja California Sur, shell drift at Punta Abrejos.

Materials examined: The type material and MEXICO: Pacific side of Baja California Norte, Isla Cedros, 1.6 km (1 mile) N of Cedros Village, 5–8 m depth, 28°06'N, 115°10'W, 2 shells (LACM 67-65.10); Pacific side of Baja California Sur, Cabo Thurlow, 27°37.5'N, 114°14.9'W, 15–20 m depth, 4 shells (LACM 71-170.9); Pacific side of Baja California Sur, Punta San Pablo, 27°12.5'N, 114°28.9'W, 20–30 m, 1 shell (LACM 71-178.14); Pacific side of Baja California Sur, Isla Asunción, E Anchorage, 27°06'N, 114°17'W, 8–23 m, 3 shells (LACM 67-66.13); Golfo de California, Baja California Sur, Bahia Concepcion, 26°42'N, 111°55'W, shallow depth, 17 shells (LACM 63-37.4); Pacific side of Baja California Sur, Bahia Magdalena, Man of War Cove, 24°37.5'N, 112°7.5'W, 0–12 m depth, 1 shell (LACM 71-183.10); Sinaloa, Mazatlan, N of Olas Altas Lighthouse, 23°12'N, 106°27'W, intertidal, 1 shell (LACM 46-9.1); Sinaloa, vicinity of Mazatlan, 23°11'N, 106°26'W, 0–6 m, 4 shells (LACM 63-11.15); Nayarit, 72 km (45 miles) NW of San Blas, Isla Isabela, 21°51'N, 105°55'W, 10 m depth, 1 shell (LACM 67-9.1). COSTA RICA: Puntarenas Province, Islas Tortugas, 1 km W of Isla Alcatraz, 09°47'N, 84°53.5'W, 2–8 m depth, 9 shells (LACM 72-46.16); Puntarenas Province, Bahia Ballena, 2 km (1.5 miles) E of Punta Ballena, 09°44.3'N, 84°33.8'W, 3–16 m depth, 8 shells (LACM 72-42.20); Puntarenas Province, Bahia Ballena, 09°44'N, 84°33'W, 1–13 m depth, 65 specimens (D. Shasky collection); Puntarenas Province, Bahia Herradura, 09°38.8'N, 84°41'W, 10–12 m depth, 2 shells (LACM 72-52.21); Puntarenas Province, Bahia Herradura, 09°38.0'N, 84°40.5'W, 23 m depth, 4 shells (LACM 72-53.5); Puntarenas Province, Islets off Punta Quepos, 09°22.7'N, 84°09.7'W, 13–25 m depth, 9 shells (LACM 72-58.21). PANAMA: Canal Zone,

off sandspit leading to Isla Venado, 08°53'N, 79°36'W, intertidal, 1 shell (LACM 75-54.12); Fort Amador, Isla Perico, 08°51'N, 79°35'W, intertidal, 1 shell (D. Shasky collection); Isla Vendao, intertidal, 7 shells (D. Shasky collection); Bahia de Panama, Isla Bona, Isla Otoque, 08°36'N, 79°39'W, 10–27 m depth, 1 shell (LACM 65-21.19); Bahia de Panama, Isla Taboga, 08°35'N, 79°30'W, 2–5 m depth, 2 shells (LACM 62-25.17); Archipelago de las Perlas, Isla Buyarena, 08.5°N, 79°W, intertidal, 1 shell (D. Shasky collection); Archipelago de las Perlas, Isla Pedro Gonzales, 08.5°N, 79°W, intertidal, 1 specimen (D. Shasky collection). ECUADOR: Guayas Province, Santa Elena Peninsula, NW side of Punta Ancon, 02°19.5'S, 80°54.0'W, intertidal, 1 shell (LACM 70-11.6); Guayas Province, Santa Elena Peninsula, W side of Punta Ancon, 02°19'S, 80°54'W, intertidal, 6 shells (D. Shasky collection).

Distribution: East Pacific, western Mexico to Ecuador, intertidal to 25 m depth.

Remarks: The holotype of *Leiostraca schwengelae* (Figures 1, 2) has lost most of the characteristic, tall-spined protoconch. Examination of the holotype, available only after proofreading the revision of *Hypermastus* and *Turveria* (WARÉN, 1991), made me realize the mistake and made the synonymy with *Alaba terebralis* obvious. *Alaba terebralis* was based on only a fragment with two teleoconch whorls and two whorls of the larval shell left. The syntype of *Eulima proca* is in good condition.

The height of the larval shell is about 500 μ m and it consists of slightly more than three whorls. This is almost twice the height of the larval shell of the otherwise somewhat similar species of *Turveria*. These, however, have a larger teleoconch (4–5 mm), and are broader with a relatively higher aperture.

Like many of the eulimids with a color pattern, this species has regularly appearing thin and sharp collabral lines on the whorls.

***Scalenostoma* Deshayes, 1863**

Scalenostoma DESHAYES, 1863:58. Type species, *S. carinata* Deshayes, 1863, by monotypy, La Reunion, Indian Ocean.

Remarks: Species of *Scalenostoma* inhabit cavities in living specimens of hermatypic corals in shallow water in tropical regions (WARÉN, 1980). Presumably they use their long proboscis to parasitize the surrounding polyps of the coral. They are likely to belong to the Eulimidae (but no well preserved specimens have been available for anatomical examination). If this assumption is correct, they differ from most eulimids in not parasitizing echinoderms. The association with cnidarians indicates a possibility that they are related to the Epitonidae, but the apical whorls (including the larval shell) are so similar to eulimids that they have frequently been identified as species of that family.

The species are highly variable, large, with a transparent, colorless shell up to 30 mm high. The first 8–10 whorls

look like a specimen belonging to *Vitreolina* Monterosato, 1884 (Eulimidae), 2–5 mm high, with flat whorls and twisted spire. The growth pattern then suddenly changes and the whorls become fatter and more irregularly coiled.

Scalenostoma subulata (Broderip, 1832) has been reported from Isla Cascara, Cocos Island, Costa Rica by SHASKY (1983b), who found six primary females, one secondary female, and 10 males in cavities in a piece of living coral from 25 m depth. I take this occasion to figure some of them (Figures 55–59).

Two species have been described from western Central America, *Chemnitzia rangi* de Folin, 1867, and *Scalenostoma babylonica* Bartsch, 1917, which usually have been classified in *Scalenostoma*. They do not conform with the type species, however, except in frequently having the lower whorls sharply keeled, which by itself is not a diagnostic feature. They are here transferred to *Niso* Risso, 1826, on the basis of shell characters specified below.

Niso Risso, 1826

Niso RISSO, 1826:218. Type species, *Niso eburnea* Risso, 1826, by monotypy, Pleistocene of southern Europe.

Remarks: One undescribed species of *Niso*, from New Caledonia, is known to parasitize a starfish (WARÉN, 1984b) and work is underway to describe the anatomy of that species. That species and the type species, *N. eburnea*, are very similar to *Niso interrupta* Sowerby, 1834, a western, Central American species that is used below to exemplify the characters of the genus.

EMERSON (1965) revised the West American species and McLEAN (1970) described *Niso emersoni* from Panama. HERTZ & HERTZ (1982) described *Eulimostraca attiloi* from off La Jolla, California, and commented on the similarity to *Niso*, but placed the species in *Eulimostraca* because it has almost no umbilicus. I consider this character less important than the great similarities in other details, including microsculpture, larval shell, size, and color pattern, and transfer it to *Niso*. HERTZ & HERTZ (1982) also placed *N. hipolitensis* in *Eulimostraca*, because of the lack of a well developed umbilicus. I agree with other authors (BARTSCH, 1917; EMERSON, 1965) that *hipolitensis* shows more affinity to *Niso* and suggest that it is kept there.

Niso rangi (de Folin, 1867)

(Figures 17, 20–22, 25–27, 30, 31)

Chemnitzia rangi DE FOLIN, 1867:61, pl. VI fig. 1.

Scalenostoma babylonica BARTSCH, 1917:338, pl. 45 fig. 2.

Type materials: *Chemnitzia rangi*, lost, not in BMNH, MNHN, or Biarritz (KISCH, 1959; P. Bouchet, personal communication); *Scalenostoma babylonica*, holotype and 1 paratype, USNM 127542 (Figure 20).

Type localities: *C. rangi*, Bahía de Panama, Archipelago de las Pearlás; *S. babylonica*, Baja California Sur, Punta San Hipolito.

Material examined: The type material and MEXICO: Pacific side of Baja California Sur, Punta San Pablo Anchorage, 21–24 m, 1 shell (LACM 71-177.5). EL SALVADOR: La Unión Province, Golfo de Fonseca, Isla Zacatillo, 13°18'N, 87°46'W, 2 m, 2 shells (LACM 73-57.1). COSTA RICA: Guanacaste Province, N of Bahía Potrero, Punta Penca, 10°29.3'N, 85°48.9'W, 8–13 m, 2 shells (LACM 72-38.7); Puntarenas Province, 1 km W of Isla Alcatraz, Isla Trotugas, 09°47.0'N, 84°53.5'W, 1.5–8 m, 3 shells (LACM 72-46.17); Puntarenas Province, Bahía Ballena, 2.4 km E of Punta Ballena, 09°44.3'N, 84°33.8'W, 3–16 m, 1 shell (LACM 72-42.21); Puntarenas Province, W side of Bahía Ballena, 09°44'N, 84°33'W, 6–10 m, 2 shells (D. Shasky collection); Puntarenas Province, Bahía Ballena, 09°44'N, 84°33'W, 13–15 m, 2 shells (D. Shasky collection); Puntarenas Province, off Bahía Herradura, 09°38.9'N, 84°40.9'W, 6 m, 1 shell (LACM 72-54.13); Puntarenas Province, Bahía Herradura, reef at N end of bay, 09°38.8'N, 84°40.9'W, 10–18 m, 10 shells (LACM 72-52.22); Puntarenas Province, Bahía Herradura, 09°38.0'N, 84°40.5'W, 23 m, 6 shells (LACM 72-53.6); Puntarenas Province, anchorage inside small islet, 1.5 km S of Punta Quepos, 09°22.7'N, 84°09.7'W, 23 m, 3 shells (LACM 72-57.5); Puntarenas Province, small islets off Quepos, 09°22.2'N, 84°09.3'W, 25 m, 2 shells (LACM 72-59.5); Puntarenas Province, N side of Isla del Cano, 08°43.3'N, 83°53.1'W, 8–13 m, 3 shells (LACM 72-63.28); Puntarenas Province, 2 km NW of Rincon de Osa, head of Golfo de Dulce, 08°43.3'N, 83°28.5'W, 2–16 m, 1 shell (LACM 72-71.14); Isla del Coco, 05°33'N, 87°00'W, 1 shell (coll. K. Kaiser). ECUADOR: Guayas Province, N side of Santa Elena Peninsula, E of Salinas, 02°11.5'N, 80°56.5'W, 10 m, 2 shells (LACM 66-114.4); Manabi Province, N side of Isla la Plata, 01°19'S, 81°05'W, 12–30 m, 2 shells (D. Shasky collection); Manabi Province, Isla Salanga, 01°35'S, 79°50'W, 10–15 m, 1 shell (D. Shasky collection).

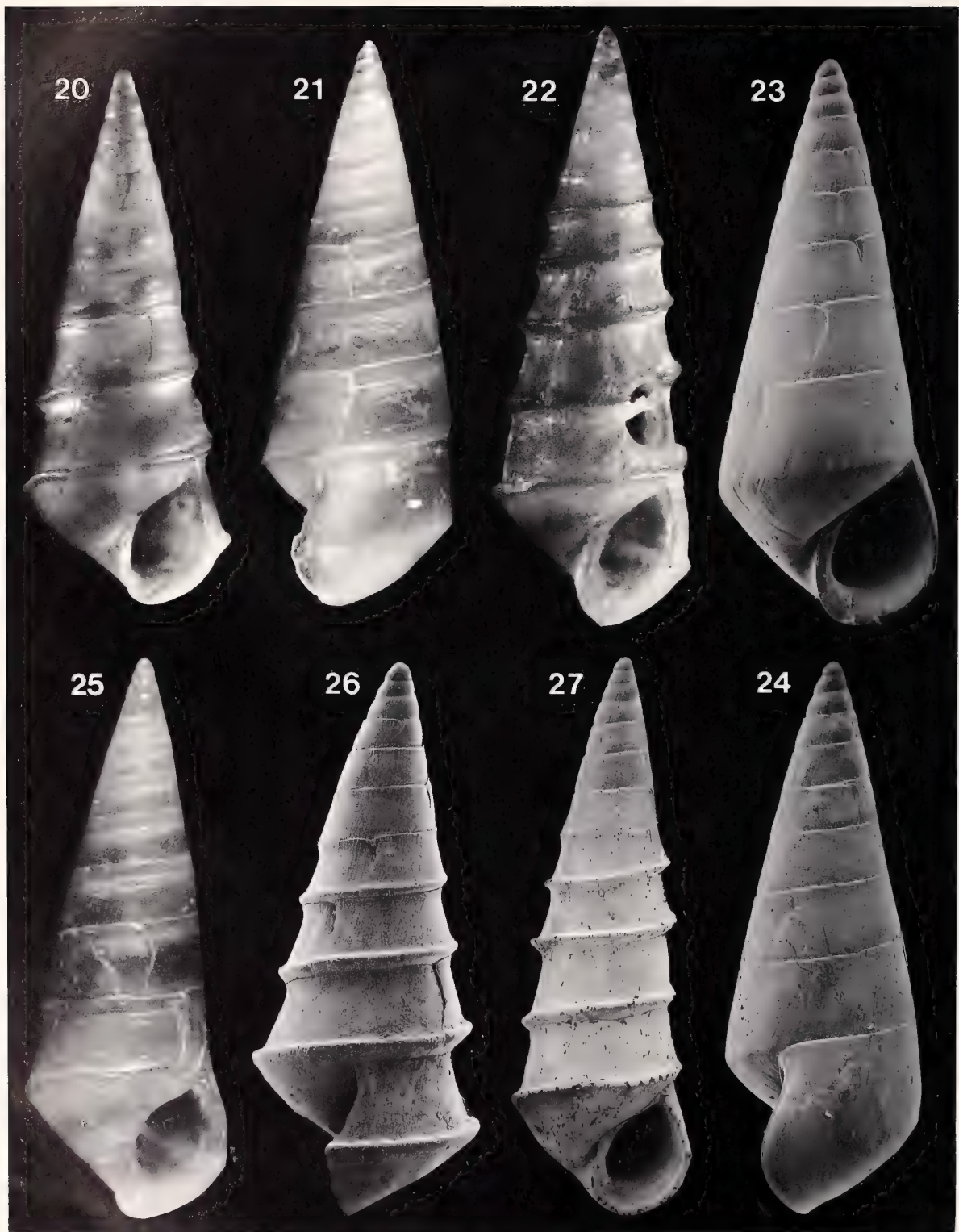
Distribution: Outer coast of Baja California Sur from about 27°N to Ecuador, also Cocos Island, in 3–30 m depth.

Remarks: *Niso rangi* is so far known only from empty shells, which makes classification more difficult. For eulimids, however, the shell is unusually rich in characters, which allows the determination of some relationships.

Figures 20–22, 25–27, 30, and 31 show the variation of the shell and that the development of the peripheral keel varies with size and the individual. In addition to what is shown by these figures, it should be mentioned that the shell is dark and dull reddish or yellowish brown.

BARTSCH (1917) had access to only two shells when proposing *Scalenostoma babylonica* and DE FOLIN's (1867) drawing is erroneous since it shows all whorls as keeled, although the shell was described as having only the last four whorls keeled. That is evidently the reason why BARTSCH (1917) described *N. babylonica*.

Examination of the larval shell (Figure 17) shows that it consists of about 3.5 whorls and has a distinct sculpture



Explanation of Figures 20 to 27

Figure 20. *Niso rangi*, holotype of *Scalenostoma babylonica*, USNM 127542, height 3.0 mm.

Figure 21. *Niso rangi*, Costa Rica, LACM 72-52.22, 2.92 mm.

Figure 22. *Niso rangi*, Costa Rica, LACM 72-59.5, 3.54 mm.

of very fine collabral lines and a height of almost 400 μm . The whole teleoconch is covered by equally sharp but straighter axial lines.

Protoconch sculpture, as well as the color, agrees closely with these features in species of *Niso*. I have exemplified that genus with a young specimen of *N. interrupta* (Sowerby, 1834), a Central American species typical for its genus (shell, Figure 28; larval shell, Figure 18; sculpture, Figure 15) and *N. hipolitensis* Bartsch, 1917 (shell, Figures 23, 24, 29; larval shell, Figure 19).

Both *Niso hipolitensis* and *N. rangi* are unusual among the species of *Niso* in their small size, 3–4 mm shell height, whereas most species of the genus have a shell that is 10–30 mm high, occasionally even higher. Nevertheless I feel satisfied with this systematic position, although it remains to be checked by examination of the soft parts, when such become available.

Niso hipolitensis can be distinguished from young specimens of *N. rangi* by having a blunter protoconch and no trace of an umbilicus. A specimen from Isla Taboga, Panama (in the collection of D. Shasky) indicates a larger size than that given by BARTSCH (1917) namely 4 mm. Had it not been that *N. hipolitensis* was a much more rare species compared with *N. rangi*, I would not have excluded the possibility of the two names having been based on the male and female, respectively, of the same species.

Eulimostraca Bartsch, 1917

Eulimostraca BARTSCH, 1917:333. Type species, by original designation, *Eulimostraca galapagensis* Bartsch, 1917, Galapagos (Figures 12, 33, 35).

Remarks: BARTSCH (1917) placed a single species in *Eulimostraca* when he introduced this generic name, but the genus is represented by several, mostly undescribed species in the Caribbean and western America. Nothing is known about the identity of the hosts of these species.

The species of *Eulimostraca* resemble *Microeulima*, but species of *Eulimostraca* have a proportionally larger and expanded aperture, giving the shell a regularly conical appearance. The aperture is, however, less expanded and more similar to *Microeulima* in young specimens, which indicates that they are related. Also, the larval shells are similar.

Eulimostraca macleani, described below, differs from the typical appearance, but has an aperture very similar to that of *E. galapagensis* and is provisionally included here.

Leiostraca linearis CARPENTER, 1857 (p. 440) (from Ma-

zatlán, Sinaloa, Mexico) was based on a small (1.84 \times 0.56 mm) specimen, similar to *Eulimostraca galapagensis*. The holotype has no trace of color pattern, but is otherwise well preserved and differs from *E. galapagensis* by having perfectly flat whorls, by having a slightly more cylindrical shell, and correspondingly by having a smaller aperture. It was figured by BARTSCH (1917:pl. 36, fig. 4), BRANN (1966:pl. 48, fig. 554), and KEEN (1968:text fig. 32, possibly also 1971:fig. 727), and the holotype is in BMNH, Mazatlán collection No. 2025.

Eulimostraca attilioi Hertz & Hertz, 1982, was discussed under *Niso* and transferred to that genus.

Eulimostraca galapagensis Bartsch, 1917

(Figures 12, 33, 35)

Eulimostraca galapagensis BARTSCH, 1917:333, pl. 43, fig. 1.

Eulimostraca galapagensis: SHASKY, 1983a:29.

Eulimostraca galapagensis: HERTZ & HERTZ, 1982:74.

Type material: Holotype and 7 paratypes, USNM 251281.

Type locality: "Galapagos Islands, 72 m."

Material examined: The types and ECUADOR: Galapagos Islands, Isla Isabela, off Tagus Cove, 00°17'S, 91°23'W, 27 m, 1 shell (LACM 34-290.1); Manabi Province, Isla La Plata, 01°16'S, 81°06'W, 30–40 m, 1 shell (D. Shasky collection).

Distribution: Only known from the material examined, Galapagos Islands, 27–72 m depth; also Corinto and Manabi Province, Ecuador.

Remarks: *Eulimostraca galapagensis* can be recognized by its distinctly conical shape and evenly yellowish color in fresh specimens. The periphery is encircled by a darker band.

I have verified SHASKY's (1983a) record by direct comparison with the paratypes.

Eulimostraca burragei (Bartsch, 1917)

Strombiformis burragei BARTSCH, 1917:345, pl. 47 fig. 5.

Melanella panamensis BARTSCH, 1917:311, pl. 36 fig. 1.

Type materials: *Melanella panamensis*, holotype USNM 251312; *Strombiformis burragei*, holotype USNM 267582.

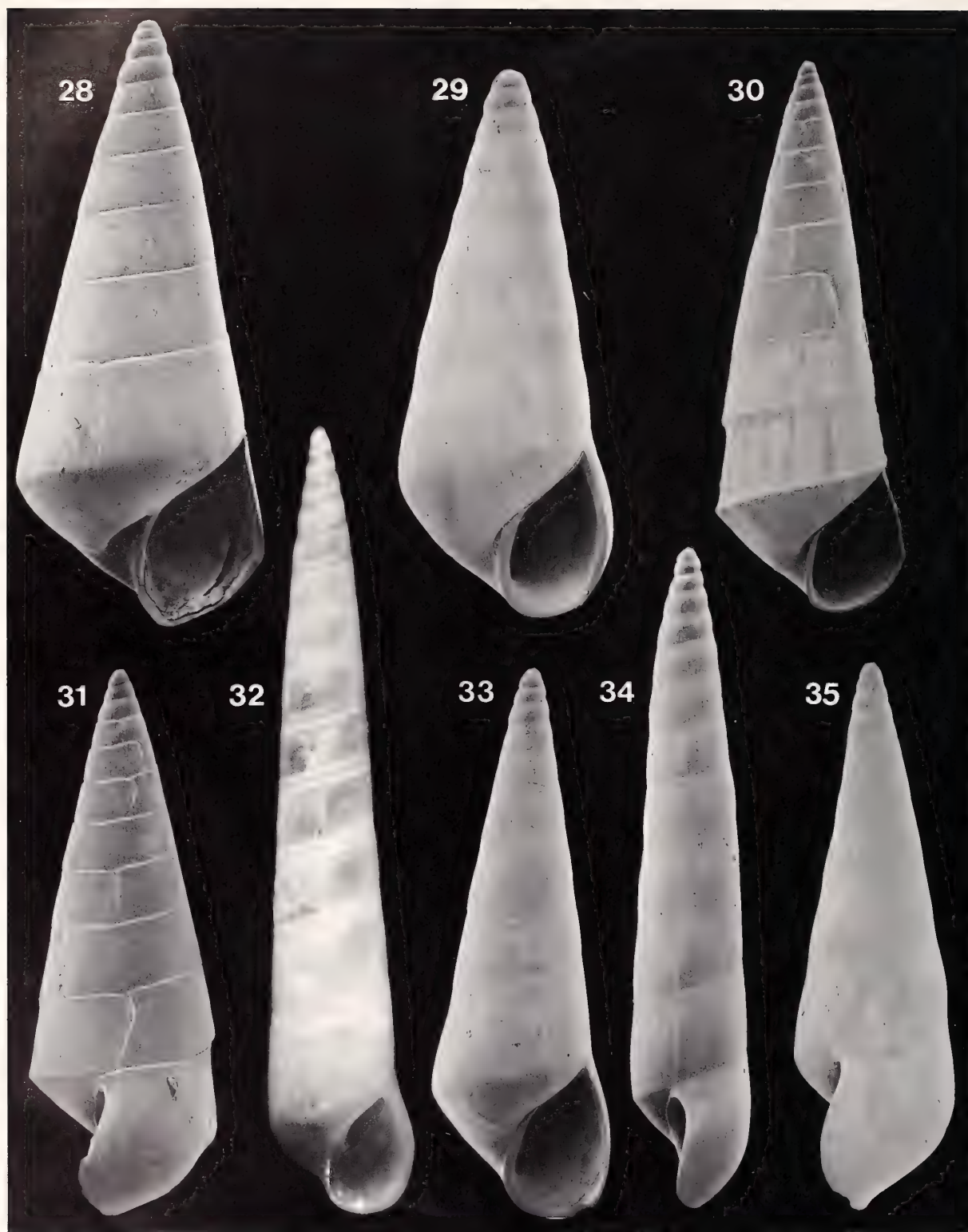
Type localities: *Melanella panamensis*, Bahia de Panama, 110 m; *Strombiformis burragei*, Bahia Concepcion, Golfo de California, 5 m.

Figures 23 and 24. *Niso hipolitensis*, Mexico. Baja California Sur, Punta Palmilla, intertidal, LACM 66-11.5, 2.3 mm.

Figure 25. *Niso rangi*, Costa Rica, LACM 72-38.1, 3.20 mm.

Figure 26. *Niso rangi*, Costa Rica, LACM 72-52.22, 2.68 mm.

Figure 27. *Niso rangi*, Costa Rica, LACM 72-63.28, 3.7 mm.



Explanation of Figures 28 to 35

Figure 28. *Niso interrupta*, LACM 55558, same specimen and data as Figure 15, 4.9 mm.

Figure 29. *Niso hipolitensis*, Galapagos Islands, Isla Isabela, off Tagus Cove, 144 m, LACM 34-290.2, 2.4 mm.

Distribution: Only known from the type specimens, from Golfo de California and Bahía de Panama, in 5–110 m.

Remarks: Examination of the two holotypes of the two names cited in the synonymy did not reveal any differences between them, except for one being more worn. The aperture is less expanded and more ovate than in *Eulimostraca galapagensis*, but this may be because the specimens are not fully mature. If this is the case, I believe the names to be synonyms of *E. galapagensis*. This would not be the first time Bartsch described the same species in three different genera.

As first reviser, I prefer to use the name *burragei* since *panamensis* invites confusion with *Strombiformis panamensis* Bartsch, 1917, a distinct species belonging to *Eulima*.

Eulimostraca macleani Warén, sp. nov.

(Figures 11, 32, 34, 40)

Type material: Holotype LACM 2370 and one paratype LACM 2371.

Type locality: Costa Rica, Puntarenas Province, Bahía Herradura, 09°38.0'N, 84°40.5'W, 23 m, LACM 72-53.

Material examined: Only known from the type lot.

Distribution: Only known from the type locality, Costa Rica, in 23 m depth.

Etymology: Named after Dr. James H. McLean, LACM, who always has been very helpful during my visits at the museum.

Description: The shell (Figures 32, 34) is very tall and slender, cylindrical, colorless(?), and transparent, except for a faint brown line along the outer lip and a more distinct blotch on the lower part of the columella. The larval shell (Figure 11) is pointed, with 2.5 perfectly smooth and evenly convex whorls, distinctly demarcated from the teleoconch. The holotype has 11.6 teleoconch whorls, of which the most apical 2 whorls are almost as convex as those of the larval shell and of more rapidly increasing diameter than later whorls. After these, the whorls gradually become flatter and the shell more cylindrical. The body whorl is distinctly angulated at the level of the suture. Starting on the second teleoconch whorl, the surface is covered by a fine spiral striation (Figure 40), barely visible under a good stereomicroscope, and only in patches where incident light is reflected. There are also scattered, occasionally sharp and distinct, usually less distinct, incremental lines. In addition, there are several incremental scars on the apical 3 whorls, then 4 not very distinct in-

cremental scars—5.9, 7.8, 10.1, and 10.6 whorls from the larval shell; but in the paratype the positions are different. The aperture is rather broad, with a distinct subsutural sinus in the outer lip. The parietal wall has a thick callus (inner lip).

Dimensions. Height of the holotype (largest specimen) 6.97 mm.

Remarks: *Eulimostraca macleani* is probably the most cylindrical eulimid known. I am not aware of any similar species from western America.

Eulimetta Warén, gen. nov.

Type species: *Eulimetta pagoda* sp. nov.

Diagnosis: Very small (ca. 2 mm) eulimid, with a brownish shell and a very strong, periodically expanding peripheral keel on the lower whorls.

Etymology: Diminutive of *Eulima*.

Remarks: The development of the keels varies. In one shell it starts almost immediately after the larval shell (Figure 37), but in most specimens it seems not to reach full development. This may be because I have failed to recognize that more than one species is involved, or the cause may be that environmental factors direct the development, as is common in eulimids (see Introduction).

Eulimetta must be rather closely related to *Eulimostraca* and *Microeulima*, judging from the shape of the larval shell and the aperture, but I prefer to make a new genus for this strangely shaped species. No other eulimid has a similar expansion of the peripheral keel.

Eulimetta pagoda Warén, sp. nov.

(Figures 14, 36–39, 41)

Type material: Holotype LACM 2372 and two paratypes and LACM 2373.

Type locality: Mexico, Jalisco, Bahía Cuastocemate, 4.8 km (3 miles) NW of Barra de Navidad, 19°13.8'N, 104°44.9'W, 18–36 m, LACM 68-45.

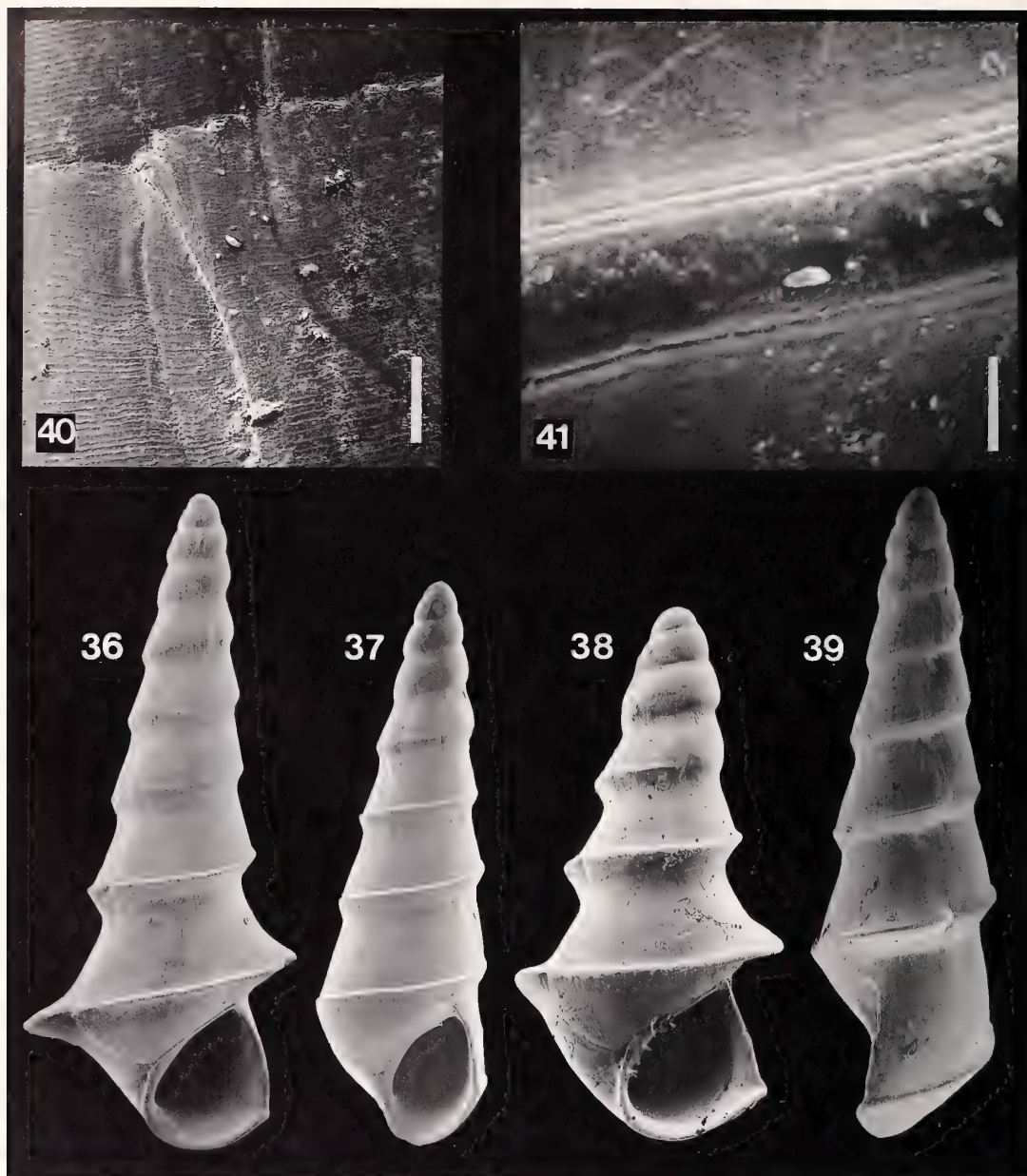
Material examined: The type material and MEXICO: Baja California Norte, 16 km S of Bahía San Luis Gonzaga, Punta Final, 29°48'N, 114°17'W, 36 m, 1 shell (LACM 61-6.3); Baja California Sur, off S end of Isla Espíritu Santo, 24°23'N, 110°20'W, 44 m, 1 shell (LACM 36-140.1); ca. 64 km (40 miles) S of Mazatlan, 22.5°N, 106.5°W, 30–35 m, 2 shells, from shrimp trawler (LACM 60-20.1); Jalisco, E of Punta Mita and off La Cruz, Bahía

Figures 30 and 31. *Niso rangi*, Costa Rica, LACM 72-52.22, 3.8 mm and 3.0 mm.

Figure 32. *Eulimostraca macleani*, holotype, LACM 2370, 6.97 mm.

Figures 33 and 35. *Eulimostraca galapagensis*, syntype, USNM 251281, 3.5 mm.

Figure 34. *Eulimostraca macleani*, paratype, LACM 2371, 6.0 mm.



Explanation of Figures 36 to 41

- Figure 36. *Eulimetta pagoda*, holotype, 2.0 mm.
 Figure 37. *Eulimetta pagoda*, Guatemala, LACM 38-25.10, 1.12 mm.
 Figure 38. *Eulimetta pagoda*, Costa Rica, LACM 72-43.4, 1.68 mm.
 Figure 39. *Eulimetta pagoda*, paratype, 2.2 mm.
 Figure 40. *Eulimostraca macleani*, paratype. Scale line 0.05 mm.
 Figure 41. *Eulimetta pagoda*, paratype, keel. Scale line 0.01 mm.

Bandera, 20°45'N, 105°25'W, 3–5 m, 4 shells (LACM 65-16.47); Jalisco, Bahia Tenacatita, 19°17'N, 104°49'W, 1 shell (LACM 33-138.1); Jalisco, Bahia Cuastecomate, 19°13.8'N, 104°44.9'W, 18–36 m, 2 shells (LACM 2373).

GUATEMALA: off Punta San Jose, 13°46'N, 91°14'W, 36 m, 1 shell (LACM 38-25.10). COSTA RICA: Puntarenas Province, off Bahia Balena, 10°44.1'N, 84°59.5'W, 12 m, 1 shell (LACM 72-43.4).

Distribution: From Baja California Norte, 29°N, to Costa Rica, in 3–44 m depth.

Etymology: Named after the pagoda-like appearance of the lower whorls.

Description: The shell (Figures 36–39) is very small, very slender, chestnut brown, fairly solid, with the angulated periphery of the whorls often developed into a winglike keel. The larval shell (Figure 14), which is 210 μ m high, has about 3.5 evenly rounded whorls with indistinct but sharp growth lines. The holotype has 5.5 teleoconch whorls, which except for the regularly appearing growth scars 0.5, 1.0, 1.5, and 2.0 whorls from the outer lip, have no sculpture visible with a stereomicroscope. Under SEM there are a few impressed spiral lines paralleling the peripheral keel (Figure 41) and the whole surface is covered by very small and shallow pits. Directly after the rather indistinctly demarcated protoconch starts a rounded keel, formed by a distinct bend in the profile of the whorl. This continues mostly unchanged for 1–4 whorls, after which it becomes more pronounced and keel-like, and transforms into a raised rib. Shortly before the outer lip it becomes lower again, a process that is repeated at each incremental scar; after an incremental scar the keel rapidly reaches maximum development. As a consequence of this growth pattern the shell looks strongly flattened, when observed from the side. The aperture is pear-shaped, with a small internal dent corresponding to the keel. The parietal callus is thick.

Dimensions. Height of holotype 2.02 mm, maximum diameter of body whorl 0.81 mm, minimum diameter of body whorl 0.54 mm; maximum height 2.32 mm.

Remarks: I am not aware of any species that can be confused with specimens with a developed keel; those with a poorly developed keel may possibly be confused with various species of *Microeulima*, unless care is taken to look for the fine and sharp (but often indistinct) axial lines of those species.

Sabinella Monterosato, 1890

Sabinella MONTEROSATO, 1890:160. Type species, *Eulima piriformis* Monterosato, 1875 (not Brugnone, 1873) = *Eulima bonifaciae* Nordsieck, 1974, Mediterranean, parasitic on test of *Cidaris cidaris* (Linnaeus, 1758).

Remarks: Several species of *Sabinella* are known to parasitize cidaroid sea urchins (WARÉN, 1984b; BOUCHET & WARÉN, 1986; WARÉN & MOOLENBEEK, 1989; WARÉN & MIFSUD, 1990) in galls in the spines or attached to the test.

The following species were placed in *Sabinella* by BARTSCH (1917):

—*Sabinella chathamensis* Bartsch, 1917. This species does not belong to *Sabinella*, but is related to the Caribbean species "*Eulima*" *hians* Watson, 1883. It is probably better to provisionally place *chathamensis* in *Eulima*, a genus comprising a very heterogenous mixture of eulimids, and keep

Sabinella as a monophyletic genus for this small group of cidaroid parasites.

—*Sabinella bakeri* Bartsch, 1917. This species probably is an eulimid despite having a rather fragile and irregular shell. I have examined a specimen with dried soft parts, and it has a ptenoglossate radula, similar to species of *Eulima*. It can provisionally be placed in *Eulima*.

—*Sabinella opalina* (de Folin, 1867). There is a possible syntype in the Museum of Comparative Zoology, Harvard University, No. 288749, which belongs in the genus *Melanella*.

—*Sabinella ptilocrinicola* Bartsch, 1907. WARÉN (1984b) placed this species in *Crinolamia* Bouchet & Warén, 1979. It lives on deep-sea crinoids.

—*Sabinella meridionalis* Bartsch, 1917, can provisionally be placed in *Eulima*.

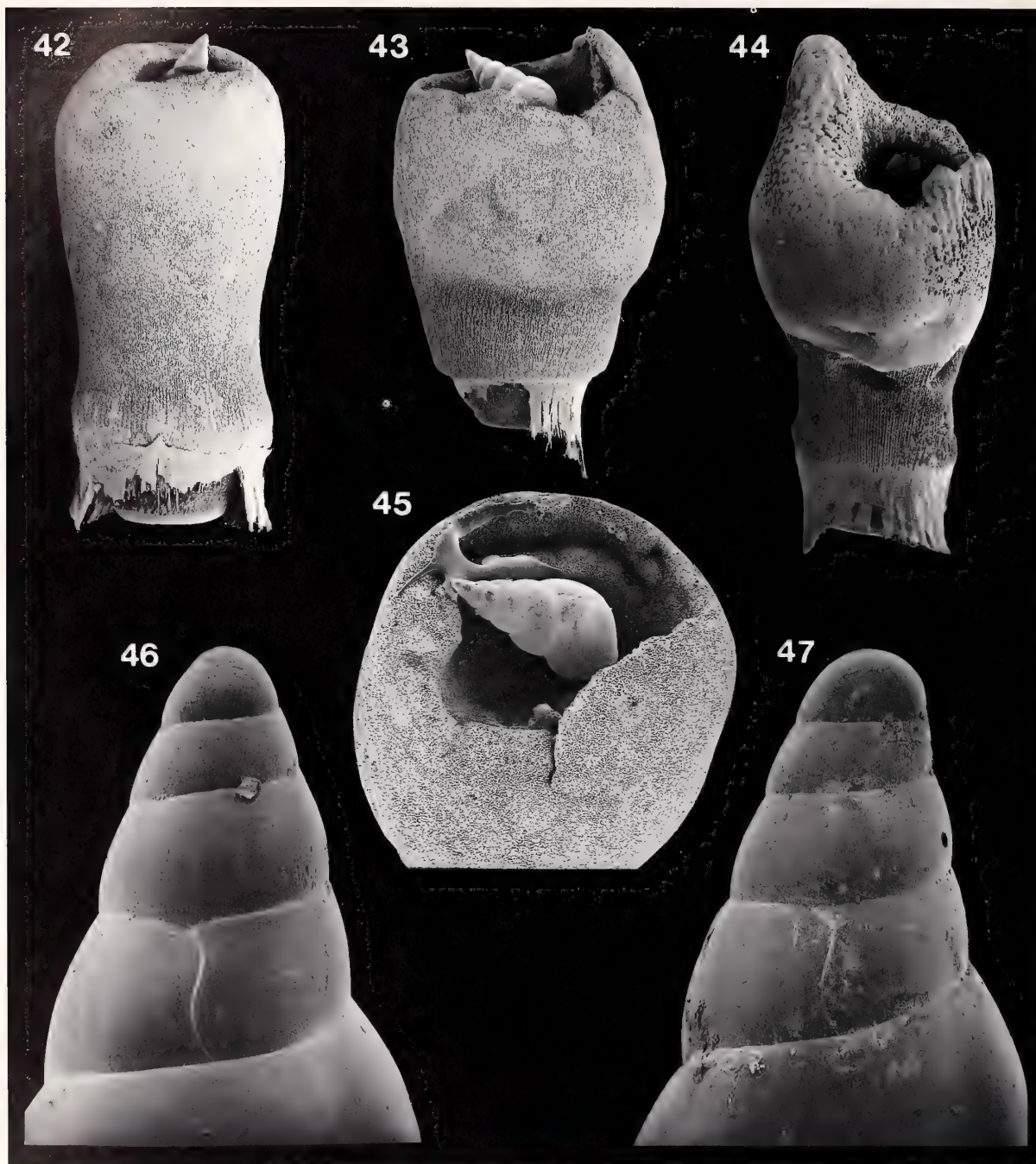
Sabinella shaskyi Warén, sp. nov.

(Figures 42–46, 48–52)

Type material: Holotype LACM 2374, 7 paratypes LACM 2375, 10 paratypes in D. Shasky collection, 12 paratypes SMNH 4378. All paratypes from Baja California Sur, El Pulmo Reef (see below).

Type locality: Mexico, Jalisco, 4.8 km (3 miles) NW of Barra de Navidad, 19°13.7'N, 104°44.8'W, 18–36 m, in a gall in a spine of *Eucidaris thourarsi* (Valenciennes, 1846), LACM 68-45.

Material examined (host *Eucidaris thourarsi*): MEXICO: Baja California Sur, El Pulmo Reef, 1.5–3 m, several host specimens, 11 males, 14 females, 6 specimens left in galls (D. Shasky collection, paratypes in LACM and SMNH); Baja California Sur, off N end of Isla San Pedro Nolasco, 27°59'N, 111°24'W, 10 m, 1 shell (LACM 73-133); Baja California Sur, SE of Isla San Pedro Nolasco, 27°59'N, 111°24'W, 17–23 m, 1 shell (D. Shasky collection); Baja California Sur, Mulegé, rocky point in front of La Serenidad, 27°00'N, 111°58'W, 3 m, 2 empty galls (+ 1 specimen of *Nanobalcis* sp. nov.) (D. Shasky collection); Jalisco, Cuastecomate, 19°13.8'N, 104°44.9'W, 5–6 m, 1 apical spine with a gall with 1 male, 2 females, and egg capsules (D. Shasky collection); Nayarit, Isla Maria Madre, 1.6 km (1 mile) S of Puerto Ballena, 21.6°N, 106.5°W, 3–5 m, 3 assumed males from 1 host (D. Shasky collection); Nayarit, Banderas Bay, Islas Tres Marias, 20°45'N, 105°30'W, 5–10 m, on host, 1 apical spine with a small, healed gall, 1 dorsal spine with a gall with male, female, and egg capsules (LACM 65-14.7). COSTA RICA: Isla del Coco, Baja Alcyone, 05°33'N, 87°00'W, 32–35 m, 2 hosts, each with 2 galls, each with male and female; 1 host with 2 specimens, no gall (D. Shasky collection); Isla del Coco, 05°33'N, 87°00'W, 21 m, 1 host with 1 healed gall, 1 gall with 2 males, 1 female (D. Shasky collection); Isla del Coco, Bahía Chatham, Punta Ulloa, 05°33'N, 87°00'W, 14–20 m, 1 young specimen 1.5 mm, no gall (D. Shasky



Explanation of Figures 42 to 47

Figure 42. *Sabinella shaskyi*, Costa Rica, Baja Alcyone, length of spine 6 mm.

Figure 43. *Sabinella shaskyi*, Mexico, Coastocomate, diameter of spine 5 mm.

Figure 44. *Sabinella shaskyi*, Cocos Island, 21 m, length of spine 6 mm. This spine is regenerating, with three new points protruding from the rim of the gall.

Figure 45. *Sabinella shaskyi*, apical view of Figure 43, shell 2.5 mm.

Figure 46. *Sabinella shaskyi*, Mexico, Coastocomate, height of larval shell 450 μ m.

Figure 47. *Sabinella troglodytes*, from *Eucidaris tribuloides*, Florida, off Cedar Key, 28°47.5'N, 84°37'W, 43 m, USFC station 2407, height of larval shell 430 μ m.



Explanation of Figures 48 to 54

Figure 48. *Sabinella shaskyi*, Mexico, Cuastecomate, D. Shasky collection, 3.6 mm.

Figures 49 and 50. *Sabinella shaskyi*, Mexico, El Pulmo Reef, D. Shasky collection, 3.0 mm and 2.9 mm, respectively.

Figures 51 and 52. *Sabinella shaskyi*, holotype, LACM 2379, 3.0 mm.

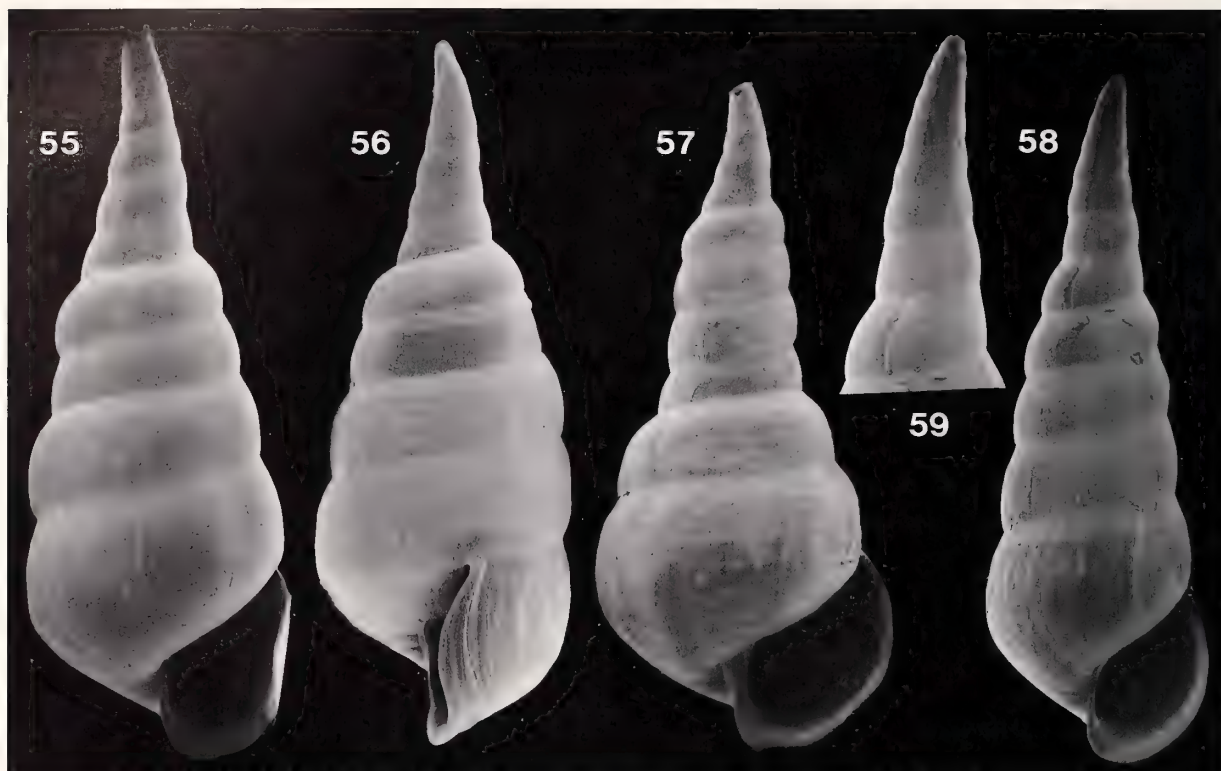
Figures 53 and 54. *Sabinella troglodytes*, USFC station 2407, for data see Figure 47, 2.2 and 3.1 mm, respectively.

collection); Isla del Coco, Isla Manuelita, 05°33'N, 87°00'W, 13–17 m, 1 shell (D. Shasky collection); Isla del Coco, Isla Manuelita, 05°33'N, 87°00'W, 100–105 m, 1 shell (D. Shasky collection). ECUADOR: Galapagos Islands, Isla Marchena, 0°18'N, 90°30'W, 6 m, 1 shell (LACM 34-285.1); Galapagos Islands, Isla Isabela, Tagus Cove, 0°16'S, 91°23'W, 15 m, 1 shell (LACM 33-165.1); Galapagos Islands, Isla San Salvador, James Bay, 0°12'S, 90°52'W, 45 m, 1 shell (LACM 34-273.1); Manabi Prov-

ince, N side of Isla La Plata, 01.1°S, 81.1°W, 10–27 m, in siftings, 2 small males, 1.6–1.7 mm (D. Shasky collection).

Distribution: From Ecuador, the Galapagos Islands, and Cocos Island north to Gulf of California, in about 5–45 m depth.

Etymology: Named after Dr. D. R. Shasky, who contributed much of the material of this study.



Explanation of Figures 55 to 59

Figures 55–59. *Scalenostoma subulata*. Costa Rica, Cocos Island, D. Shasky collection. Figure 55. Assumed primary female, lacking penis, height of shell 10.4 mm. Figure 56. Assumed primary female, with penis, height of shell 10.1 mm. Figure 57. Assumed secondary female, with penis, height of shell 11.3 mm. Figures 58 and 59. Assumed male, with penis, height of shell 8.0 mm. Figure 59. Apex enlarged, showing labial scar marking transition from normal eulimid to “*Scalenostoma* shape.” The soft parts were too decayed to check for the presence of a pallial oviduct.

Description: *Female*. The shell (Figures 48–52) is small, grayish white, semitransparent, conical, somewhat irregularly coiled, usually with a slightly twisted or curved spire. The larval shell (Figure 46) is multispiral and distinctly demarcated from the teloconch. The height is 450 μm . It has about 3.3 perfectly smooth whorls of rapidly increasing diameter and protoconch 1 is hardly discernible. The teloconch of the holotype has 4.5 whorls with distinct incremental scars 0.7, 1.4, 2.3, 3.0, 3.5, and 3.9 whorls from the larval shell, but the distance between them is subject to much individual variation. The whorls are quite convex with a shallow but distinct suture. The subsutural zone is not very distinct and occupies $\frac{1}{4}$ – $\frac{1}{5}$ of the height of the whorls. The surface of the shell is perfectly smooth under a stereomicroscope, except for more or (usually) less distinct growth lines. Under SEM a fine striation, consisting of 4 fine rows of granulae per 10 μm , is visible. The aperture is almost triangular, pointed anteriorly and posteriorly. The outer lip is strongly protruding in its adapical part, most so at $\frac{1}{3}$ of its height, counted from the suture.

Dimensions. Height of holotype 2.96 mm, maximum height 3.6 mm.

Male. The shell resembles that of the female but is slightly more slender, with a straighter spire, and is smaller, $\frac{2}{3}$ of the height of the female.

Galls (Figures 42–45). Various developed, depending on how long the host has been parasitized. Galls start as a simple lateral or apical depression on a normal-looking spine, inhabited by one or two young specimens. The spine then gradually becomes thicker by a change in its growth pattern and at the same time the depression becomes deeper. Finally the spine may become completely hollow, with a narrow, apical, or lateral pore, and the diameter of the gall may be twice the diameter of a normal spine.

Remarks: DÖDERLEIN (1887) figured and MORTENSEN (1928:397) mentioned the galls, noticed in specimens of *Eucidaris thourarsi* from Galapagos and Panama, but they were not aware of the cause.

SHASKY (1967) recorded this species under the name “*Rosenia nidorum* (Pilsbry, 1956),” from Baja California, an identification WARÉN (1984b) considered erroneous.

Sabinella shaskyi, however, closely resembles *S. troglodytes* (Thiele, 1925) (= *Mucronalia nidorum* Pilsbry, 1956) (Figures 53, 54) from the Caribbean area and off West Africa. The two species can be distinguished mainly by the larval shell (Figure 47), which is more slender with flatter whorls in *S. troglodytes*.

Scattered large specimens (Figures 49, 50), of which one was confirmed to be a female, differ in having a less regularly coiled shell and distinct incremental lines. The larval shell is identical with that in normal specimens and I believe this to be individual variation.

All the specimens reported above, as well as the hosts, were dried, which made it difficult to make any observations on the soft parts. Furthermore, some of the snails had fallen out of the galls and additional small specimens may have been lost. A few selected specimens from galls were rehydrated, however, and three specimens smaller than 2 mm were confirmed to be males on the basis of a large penis. Three specimens larger than 2 mm but without a penis were assumed to be females. This conforms to the observations on three other species of *Sabinella* (WARÉN, 1984b; BOUCHET & WARÉN, 1986).

In one case the occurrence of two females and a single male in a gall was confirmed, but no conclusions about the proportions of the sexes or the normal numbers of individuals per gall can be drawn.

Two specimens, 1.6 mm high and presumably males, were found free in a sediment sample taken in Ecuador. This indicates that the males may be able to leave the galls for courting.

Occasionally the galls are found empty or with empty shells inside, which indicates that the parasite probably has a shorter life-span than the host. (I have noticed this, several times in *S. troglodytes* also.) Finally, hosts can be found with the spines in a state of repair (Figure 44), with a new point of the spine growing out apically from an empty gall. All these transformations of the spines are possible since the spine is a porously calcified, living endoskeleton, not a lifeless calcareous structure, as is a spine of a *Murex* shell.

Sabinella shaskyi produces small spherical egg capsules containing about 100 eggs and attaches them to the floor of the gall, where up to a dozen capsules have been found.

Examination of 44 specimens of *Sabinella shaskyi* showed that 25% of the 24 specimens larger than 2 mm had the apex broken off, while not a single (out of 20) specimen smaller than 2 mm had a broken apex. All specimens with a broken apex had lived in incompletely formed galls. This shows two interesting features in the biology of the species: the snails are attacked by shell-cracking predators and the galls have a protective function.

Sabinella troglodytes lives in the same way as *S. shaskyi*, on *Eucidars tribuloides* (Lamarck, 1816) in the Caribbean area and off West Africa. This host species has been assumed to be closely related to and to have diverged from *E. thouarsi* after the closing of the straits across the Central American isthmus (MORTENSEN, 1928) in the late Plio-

cene. LESSOIS (1981) investigated the morphologic and genetic variation between and within the two sea urchins and confirmed this assumption. It can therefore probably also be assumed that the two species of *Sabinella* have followed the same allopatric pattern of speciation.

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Geographic and Temporal Variation in Shell Morphology of *Acanthina* Species from California and Northern Baja California

by

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Abstract. Intraspecific patterns of geographic and temporal variation are important to understanding the processes involved in the maintenance and divergence of species. Here we examine patterns of geographic and Pleistocene–Recent temporal variation in species of the neogastropod *Acanthina* from coastal California and Baja California.

A cline of increasing shell height with increasing latitude is present among modern *Acanthina punctulata*. This pattern is similar to that observed in some other mollusk species, and may be related to temperature, growth rate, and individual longevity.

In *Acanthina spirata*, modern samples are consistently different from fossil (Late Pleistocene) samples with respect to shouldering, except that modern samples from Los Angeles appear more similar to the fossils. Modern and fossil samples also differ consistently in relative shell thickness. We believe these differences are more readily explained as genetic, rather than purely ecophenotypic. Range expansions of *A. spirata* following Pleistocene climate fluctuations may have facilitated the spread of the characteristic modern forms.

INTRODUCTION

Patterns of geographic and temporal variation within and among species are important to our understanding of how species are maintained and how they give rise to new species. Patterns of variation in organisms inhabiting an area such as the west coast of North America are of special interest because frequent tectonic activity and Pleistocene sea-level and temperature fluctuations have provided a particularly dynamic context in which both organisms and species live out their lives. The degree and type of intraspecific variation present may reflect a species' response to this dynamic physical environment.

This study analyzes data on both geographic and temporal variation within species of *Acanthina* (FISCHER, 1807; Muricacea) from the Pacific coast of California and Baja California. The genus *Acanthina* includes five extant species of rocky intertidal carnivores from the west coast of North America (WU, 1985). We examined the three most northerly (*A. spirata* (Blainville, 1832), *A. punctulata* (Sowerby, 1831), and *A. paucilirata* (Stearns, 1872); see Figures 1, 2), and focus here on the former two.

In this paper we explore the kinds of variation present

in the shell morphology of these species, and examine its geographic and temporal expression. The patterns found reflect the physical variation encountered within species' geographic ranges, and the dynamic nature of this environment through time.

MATERIALS AND METHODS

Pleistocene glacioeustatic sea level highstands left "bathtub rings" of marine terrace sediments along the coast of California and Baja California. Subsequent tectonism has elevated these deposits, sparing them from further marine erosion. Marine terraces are formed by the leading edge of the transgressive (and subsequent regressive) belt sander of erosion. These terraces are usually cut into the coastal bedrock (BRADLEY & GRIGGS, 1976), which is often well lithified in this area, creating abundant rocky intertidal habitat. The fossiliferous nearshore sediments on these terraces were probably deposited during a fall of relative sea level (BRADLEY & GRIGGS, 1976).

Correlation of marine terrace deposits in California and Baja California has received considerable attention. Many workers have used elevation above current sea level and

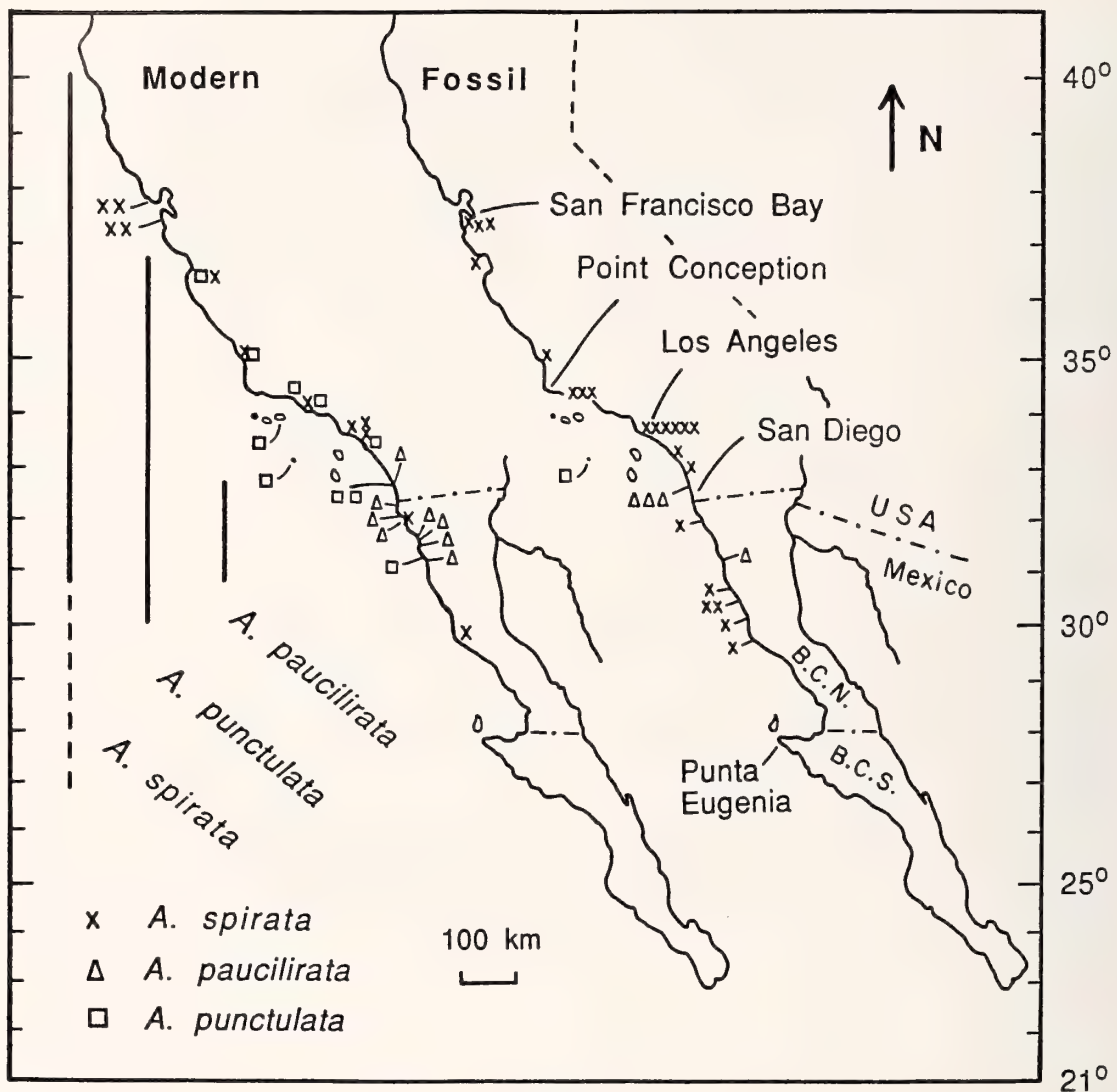


Figure 1

Index maps of the coast of California and Baja California, showing approximate collection localities of modern (left) and fossil (right) samples. Modern latitudinal ranges for species are given at left. Southern end of *Acanthina spirata* range includes scattered, rare reports as far south as Punta Abrejos, Baja California (WU, 1985). Baja California Norte (B.C.N.) and Baja California Sud (B.C.S.) are indicated at right.

the relative position within a suite of terraces at one locality to correlate terrace deposits (KANAKOFF & EMERSON, 1959; ORTLEIB, 1986; and references therein). VALENTINE (1961) and VALENTINE & MEADE (1961) developed a biostratigraphic correlation system based on the distribution of climatically sensitive extralimital southern and northern mollusk species. More recently, a variety of other techniques have been applied to the problem, including amino acid racemization (WEHMILLER *et al.*, 1977; LAJOIE *et al.*, 1979; KENNEDY *et al.*, 1982), uranium-series dating of corals (KU & KERN, 1974) and mollusks (FANALE & SCHAEFFER, 1965; SZABO & ROSHOLT, 1969), oxygen iso-

topic temperature estimates from mollusks (VALENTINE & MEADE, 1961), and an interdisciplinary approach utilizing the zoogeographic signature (warm, cool) of terrace faunas (KENNEDY, 1978; KENNEDY *et al.*, 1982; KENNEDY & WEHMILLER, 1986). Amino acid racemization dates in this region are calibrated by uranium-series dating of solitary corals from the 80 ka (= 80,000 years before present) and 125 ka highstand deposits from Oregon to Baja California (VEEH & VALENTINE, 1967; KU & KERN, 1974; ROCKWELL *et al.*, 1989; MUHS *et al.*, 1990). These relative and absolute dating techniques allow correlation with the oxygen isotope curves of SHACKLETON & OPDYKE (1973, 1976) and

sea level curves of BLOOM *et al.* (1974) and SHACKLETON (1987), placing these deposits in a well-defined temporal framework.

Species of *Acanthina* are generally well represented in the Pleistocene marine terraces of coastal California and Baja California. In addition to personal field collections, we utilized material from the Los Angeles County Museum of Natural History, the San Diego Museum of Natural History, the Santa Barbara Museum of Natural History, the California Academy of Sciences, and the University of California Museum of Paleontology, Berkeley. The fossil collections are from localities that have been correlated by other workers on the basis of the temperature affinities of the fauna, calibrated aminostratigraphic age estimates, shoreline-angle elevations, and geomorphic relationships with other deposits of known age (see Table 1).

More than 90% of our fossil *Acanthina* specimens come from the 125 ka highstand deposits of the last interglacial period. The 125 ka transgression probably removed many of the previous terrace deposits (with notable exceptions in the Palos Verdes Hills, San Diego, and Punta Banda, Baja). In the rare pre-125 ka rocky intertidal deposits, *Acanthina* is seldom preserved (owing to ground-water leaching), and almost never in the large number of well-preserved individuals desirable for morphological analysis.

In both modern and fossil samples, the largest individuals showing minimal breakage and little or no evidence of shell repair were selected for measurement. Specimens with shell height less than one-third that of the largest individual from that sample were not included, in order to minimize the potential effects of ontogenetic variation. Most modern samples contained 30 measured individuals; fossil samples typically had fewer individuals suitable for measurement (see Table 1). A total of 878 modern and 214 fossil specimens were measured.

Shells were mounted in cardboard trays in full apertural view, with the columellar axis horizontal to the tray. Measurements were made from a video image of the specimens using a digitizing pad and Bioquant software. In addition, we used modified vernier calipers to measure the thickness of the shell wall. We measured a total of eight variables and calculated an additional six ratios or shape factors (see Appendix). Variables were chosen to describe the size and shape of the shell and the aperture. We employed a variety of univariate and multivariate techniques to investigate potential patterns in the data (using SYSTAT; WILKINSON, 1988). We present here only univariate or bivariate plots, because they are easiest to interpret, and because the multivariate analyses provide no additional information or clarity in these particular cases.

We examined measurement error by remounting and measuring one specimen 20 times. Measurements subject to the most variability were those that involved tracing of the shell outline, or some portion thereof, such as shell area, or shouldering (see Appendix for standard deviations for the replicates of each variable). For all variables, mea-

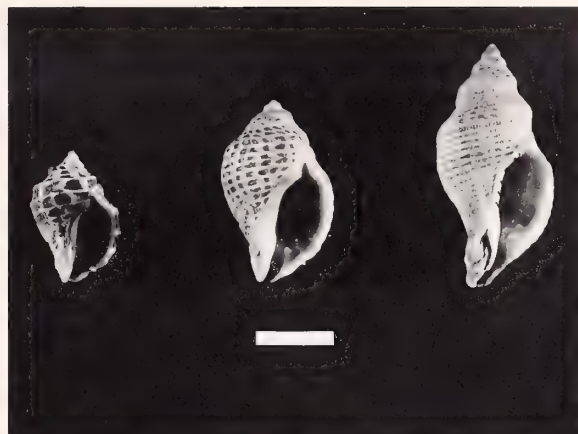


Figure 2

The three species of *Acanthina* in this study: *A. paucilirata*, *A. punctulata*, and *A. spirata*, from left to right. Scale bar is 1 cm. The characteristic labial spine is used to open the opercular plates on barnacles (YENSEN, 1979; PERRY, 1985), which, with mussels and gastropods, are the typical prey of these carnivores (SLEDER, 1981; MENGE, 1974; PERRY, 1985).

surement error is smaller than the differences among samples or species that we discuss here.

RESULTS

Distinguishing Among Species

The three species we studied are distinguished on the basis of radular and other soft-part characters (WU, 1985), which correlate with differences in shell size, shape, and color and ornamentation pattern. Although distinguishing among species was not our primary objective here, the three species separate fairly well on the basis of shell size and shape (as measured by shell height versus the ratio of shell height to width; Figure 3). In general, specimens of *Acanthina paucilirata* are the smallest and relatively most stout, whereas specimens of *A. spirata* exhibit the largest size and most slender shape.

Acanthina punctulata

Modern samples of *Acanthina punctulata* exhibit a cline of increasing shell size with increasing latitude (Figure 4). The southernmost sample and the two northernmost samples do not fit the cline. For all other samples, however, the pattern is robust. Correlation of mean shell height with latitude for these samples yields $r = 0.980$, $P < 0.001$; correlation of maximum shell height with latitude yields $r = 0.962$, $P < 0.001$; for all samples, correlation of maximum height with latitude yields $r = 0.739$, $P = 0.015$.

None of the shape variables in *Acanthina punctulata* shows this latitudinal relationship, nor is shape highly correlated with size in this species. Fossils of *A. punctulata*

Table 1

Sample, locality, sample size (*n*), age, correlation method, source, and latitude for modern and fossil samples of *Acanthina* used in this study. Method abbreviations: AA, amino acid racimization; BT, biostratigraphic temperature affinities; Phy, physical relationships; Th/U, uranium series dating; VA, volcanic ash. Source abbreviations: 1, T. A. Demere (personal communication); 2, EMERSON (1956); 3, KENNEDY *et al.* (1982); 4, G. L. Kennedy (personal communication); 5, KERN (1977); 6, KU & KERN (1974); 7, LAJOIE *et al.* (1979); 8, MUHS (1985); 9, MUHS *et al.* (1988); 10, ORTLIEB (1986); 11, SARNA-WOJCICKI *et al.* (1985); 12, WEHMILLER *et al.* (1977); 13, VALENTINE (1980); 14, VALENTINE & VEEH (1969). Museum abbreviations: CAS, California Academy of Sciences; LACM, Los Angeles County Museum; LACMIP, Los Angeles County Museum, Department of Invertebrate Paleontology; SBMNH, Santa Barbara Museum of Natural History; SDMNH, San Diego Museum of Natural History; UCMP, University of California Museum of Paleontology; UW, University of Wisconsin Geology Museum.

Sample	Locality	<i>n</i>	Age	Method and source	Museum	Catalog no.	Latitude
<i>Acanthina paucilirata</i>							
102701	Thurloe Bay, BCS	20	modern	NA	LACM	35179	27.62°N
103101	Punta Piedras, BCN	30	modern	NA	SBMNH	10461	31.37°N
103102	San Miguel, BCN	10	modern	NA	LACM	61842	31.90°N
103103	Ensenada, BCN	29	modern	NA	LACM	11358	31.85°N
103104	Punta Morro, BCN	30	modern	NA	UW	1861/5	31.86°N
103201	Tijuana Beach, BCN	30	modern	NA	LACM	62-18	32.50°N
103202	Punta Descanso, BCN	30	modern	NA	UW	1861/6	32.26°N
103203	La Jolla, CA	30	modern	NA	LACM	14007	32.85°N
103204	Rosarito, BCN	30	modern	NA	LACM	127444	32.35°N
701	Punta Loma, CA	6	120 ka	BT, AA	5 SDMNH	12923	32.66°N
702	Punta China, BCN	1	?120 ka	BT	2 UCMP	A-9002	31.50°N
704	?Punta Loma, CA	6	120 ka	BT	5 LACMIP	(UCLA 3605)	32.66°N
705	Punta Loma, CA	19	80 ka	BT, AA	9 LACMIP	11701	32.60°N
<i>Acanthina punctulata</i>							
203101	Santo Thomas, BCN	30	modern	NA	LACM	66-1	31.55°N
203201	San Diego, CA	27	modern	NA	LACM	140004	32.71°N
203301	Point Fermin, CA	21	modern	NA	LACM	63070	33.73°N
	Point Fermin, CA	9	modern	NA	LACM	60414	33.73°N
203302	San Nicolas Is., CA	30	modern	NA	LACM	60700	33.33°N
203401	Santa Cruz Is., CA	10	modern	NA	LACM	69-11	34.00°N
	Santa Cruz Is., CA	9	modern	NA	LACM	60729	34.00°N
	Santa Cruz Is., CA	10	modern	NA	LACM	60694	34.00°N
203402	Hobson Point, CA	30	modern	NA	LACM	(T&B Phillips:629)	34.33°N
203501	Shell Beach, CA	30	modern	NA	LACM	61-11	35.16°N
203502	Piedras Blancas, CA	30	modern	NA	SBMNH	02461	35.49°N
203503	Cayucos, CA	8	modern	NA	LACM	66614	35.35°N
	Cayucos, CA	22	modern	NA	SBMNH	40121	35.35°N
203601	Monterey, CA	7	modern	NA	SBMNH	66197	36.62°N
	Monterey, CA	15	modern	NA	LACM	64-2	36.62°N
	Monterey, CA	5	modern	NA	LACM	14092	36.62°N
601	San Nicolas Is., CA	19	120 ka	Th/U, AA	14, 8 LACMIP	11749	33.33°N
<i>Acanthina spirata</i>							
3001	Socorro, BCN	24	modern	NA	LACM	66-3	30.49°N
3201	Rosarito, BCN	30	modern	NA	SBNHM	10080	32.35°N
3302	Newport Beach, CA	30	modern	NA	SBNHM	10082	33.40°N
3303	San Pedro, CA	30	modern	NA	SBNHM	10082	33.74°N
3333	San Pedro, CA	30	modern	NA	LACM	140001	33.74°N
3401	Summerland, CA	30	modern	NA	SBMNH	25513	34.60°N
3501	Morro Bay, BCN	28	modern	NA	SBNHM	10078	35.33°N
3601	Del Ray, CA	30	modern	NA	LACM	60696	36.62°N
3701	San Francisco, CA	30	modern	NA	SBNHM	10077	37.97°N
3702	San Francisco, CA	23	modern	NA	LACM	62-2	37.79°N
3801	Tomales Bay, CA	30	modern	NA	LACM	AHF-1629-48	38.17°N
3802	Tomales Bay, CA	30	modern	NA	LACM	AHF-1625-48	38.10°N
901	San Francisco, CA (Merced Fm.)	5	400 ka	VA	11 CAS	6039.01	37.73°N
	San Francisco, CA (Merced Fm.)	5	400 ka	VA	11 CAS	59206.01	37.73°N

Table 1
Continued

Sample	Locality	<i>n</i>	Age	Method and source		Museum	Catalog no.	Latitude
902	San Francisco (Merced Fm.)	1	400 ka	VA	11	CAS	60404.01	37.72°N
	San Francisco, CA (Merced Fm.)	9	400 ka	VA	11	CAS	2318.01	37.72°N
903	Santa Cruz, CA	1	85 ka	AA	7	CAS	59647.01	36.95°N
904	Cayucos, CA	1	120 ka	Th/U, AA	12	LACMIP	(UCLA 3393)	35.44°N
905	Ventura (Santa Barbara Fm.)	3	>700 ka	VA	7	LACMIP	50243	34.27°N
	Ventura (Santa Barbara Fm.)	2	>700 ka	VA	7	SDMNH	29603	34.27°N
906	Sea Cliff, CA	1	5 ka	C ¹⁴ , AA	7	SDMNH	13910	34.34°N
907	Ventura Terrace, CA	9	45 ka	AA	7	LACMIP	5029	34.27°N
908	*“Railroad Depot”	30	120 ka	AA	7	CAS	91.09	33.73°N
909	*San Pedro	14	120 ka	AA	3	LACMIP	131	33.73°N
910	*San Pedro	6	120 ka	AA	3	CAS	66025.01	33.73°N
911	*San Pedro	8	120 ka	AA	3	CAS	6602.07	33.73°N
912	*San Pedro	7	120 ka	AA	3	CAS	66021.01	33.73°N
913	Camp Pendleton, CA	7	120 ka	AA	3	LACMIP	5574	33.40°N
914	La Jolla, CA	6	120 ka	AA	6	SDMNH	12547	32.82°N
915	Camalu, BCN	10	120 ka	AA, BT	13	UCSB	1143	30.83°N
916	Camalu, BCN	3	120 ka	AA, BT	13	UW	1861/1	30.83°N
917	Pta. San Telmo, BCN	11	?120 ka	Phy	10	UW	1861/2	30.93°N
918	Pta. Baja, BCN	2	?120 ka	BT, Phy	2	UW	1861/3	29.96°N
919	San Quintin, BCN	1	?120 ka	10		LACMIP	(UCLA 2411)	30.48°N
	San Quintin, BCN	3	?120 ka	10		SBMNH	16066	30.48°N
920	La Fonda, BCN	4	120 ka	AA, Phy, BT	4	UW	1861/4	32.13°N
921	San Francisco, CA	1	?400 ka	VA	11	UCMP	B-4810/37672	37.73°N
922	San Diego, CA (Bay Point Fm.)	6	?205 ka	AA	1	CAS	105.01	32.80°N

* Palos Verdes Sands, Los Angeles County, CA.

were too rare to provide significant sample sizes for morphometric analyses.

Acanthina paucilirata

We measured specimens from eight modern and four fossil samples of *A. paucilirata*. Our fossil specimens, how-

ever, exhibited considerable shell wear, which made accurate comparison of most shell characters difficult. Therefore, we believe our data are inconclusive with respect to potential trends or patterns within this species.

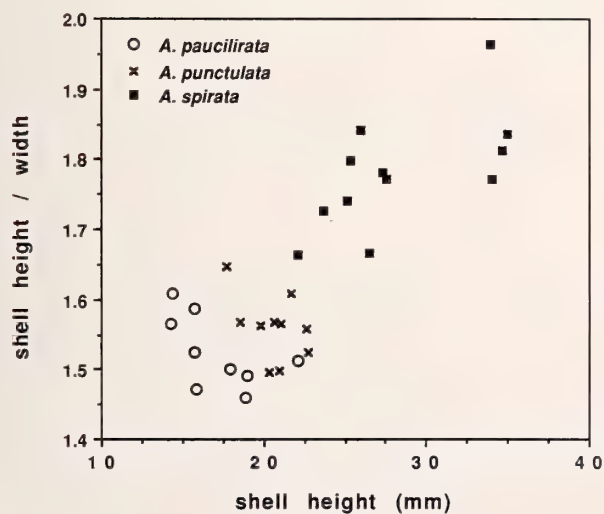


Figure 3

Sample means for all modern samples for shell height and the ratio of shell height to width.

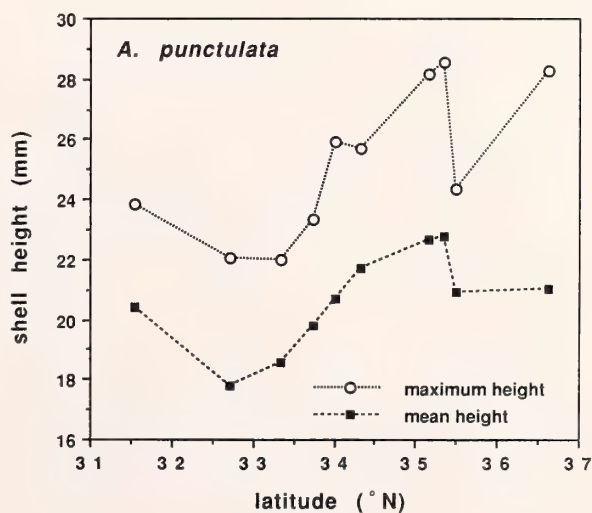


Figure 4

Relationship of shell height to latitude among modern samples of *Acanthina punctulata*. Both sample means and maximum values are shown.

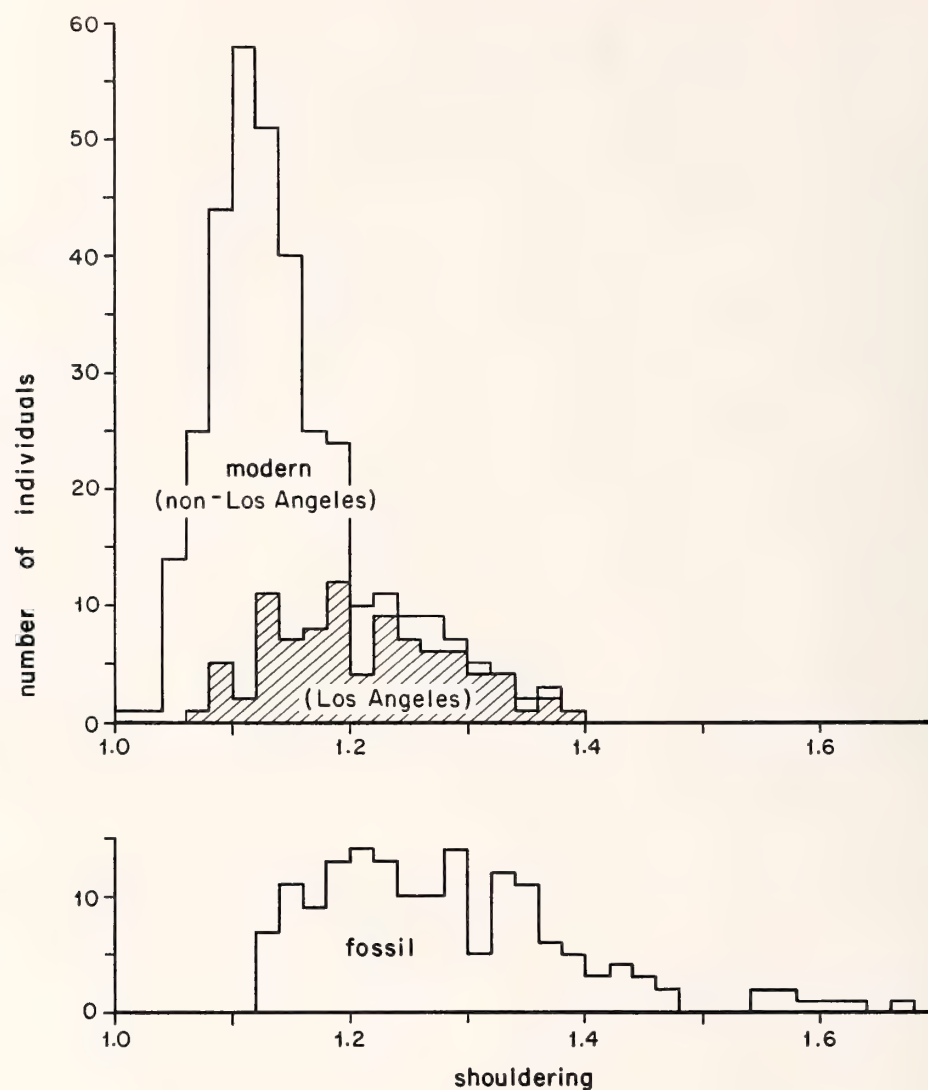


Figure 5

Histograms for shouldering for all modern and fossil specimens of *Acanthina spirata*. Shouldering is measured as the trace of the right hand shell margin from apex to body whorl suture, divided by the length of the straight line segment connecting the same two points (see Appendix). Shells with nearly straight shell profiles have lower values for shouldering; shells with pronounced development of shoulders have higher values. Means for the three groups indicated are modern non-Los Angeles (1.12), modern Los Angeles (1.21), and fossil (1.28).

Acanthina spirata

Comparison of fossil with modern samples of *Acanthina spirata* revealed at least two consistent morphological differences: (1) modern samples exhibit less pronounced shouldering than do fossil samples, with the exception of modern samples from Los Angeles, which more closely resemble the fossils; and (2) for any given shell height, modern samples have relatively thicker shells.

Differences between modern and fossil samples with respect to shouldering are shown in Figures 5 and 6. Figure 5 plots all individuals with respect to this character; Figure 6 illustrates typical fossil and modern morphologies. The

difference between fossil and modern samples is significant with a *t*-test at $P < 0.001$. Among modern specimens, those from the Los Angeles area exhibit the highest values for shouldering, and indeed, are intermediate between typical fossil and modern morphologies with respect to this character.

The relationship between shell height and shell wall thickness is plotted in Figure 7. We did not measure shell thickness on individuals that showed obvious signs of shell wear or dissolution; all samples for which shell thickness could be accurately measured are plotted in Figure 7. This plot reveals a separation of fossil from modern samples;



Figure 6

Typical specimens of *Acanthina spirata*, showing characteristic differences in shouldering between fossil (right) and modern non-Los Angeles (left) specimens. The modern Los Angeles specimen (center) more closely resembles typical fossil shouldering morphology. Scale bar is 1 cm.

fossil shells have thinner shells relative to their size than do modern shells. An analysis of covariance (ANCOVA) demonstrates that this difference in relative thickness between fossil and modern samples is significant ($P < 0.001$). Modern Los Angeles samples are indicated by +'s, but do not differ significantly from other modern samples with respect to relative shell thickness.

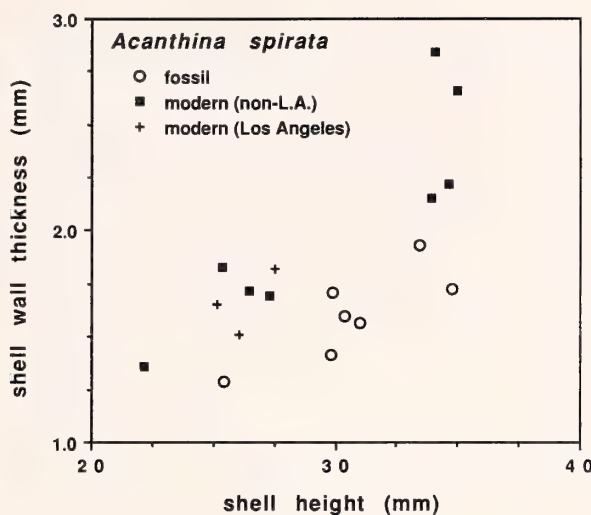
Samples of *Acanthina spirata* exhibit no other consistent patterns of geographic variation, such as the size cline observed in *A. punctulata*.

DISCUSSION

Two types of patterns are indicated in the data presented above: (1) a latitudinal size cline in *Acanthina punctulata*; and (2) time-related, and partly geographically related, differences in shell shouldering and thickness in *A. spirata*.

Cline in Shell Size in *Acanthina punctulata*

Intraspecific clines of increasing size with higher latitude such as that seen over most of the geographic range of *Acanthina punctulata* have been reported for a number of other mollusks (e.g., WEYMOUTH *et al.*, 1931; NEWELL, 1964; FRANK, 1975; see also HARRINGTON, 1987). This type of clinal variation is thought to stem from slower growth rates but increased longevity at lower temperatures, resulting in larger overall size. We have no information on individual longevity or relative growth rate in these snails, but the similarity of our pattern to that of others suggests a similar cause. The exceptional southernmost and northernmost samples of *A. punctulata* may result from unusual temperature conditions: proximity to local up-



1934; SPIGHT, 1977). The limited dispersal ability of species in this genus raises the question of how the observed differences in shell morphology spread through the range of *A. spirata*.

The pronounced paleoclimatic temperature changes that characterize the Pleistocene, and the latitudinal migrations of species ranges that resulted, may help to explain how the observed morphological shifts occurred. Rather than a direct replacement of fossil morphotypes with modern ones, the shifts in morphology may have occurred as the species spread into its current range after occupying a more restricted or only partly overlapping range during cooler (and/or warmer) intervals of the Pleistocene. Marine temperatures since 125 ka have been generally cooler than at present, and therefore the northern limit for *Acanthina spirata* was probably farther south than it is today. The population(s) that spread north to establish the current range of *A. spirata* most likely represented only a small subset of the variability that was present within the species. Whether the modern phenotype had some selective advantage during recolonization, or came to dominate simply through a kind of founder effect, is unknown. The fact that modern *A. spirata* from the Los Angeles area resemble fossil samples or are intermediate between typical fossil and modern phenotypes suggests that populations may have been maintained more continuously in this area. This hypothesis requires further testing with distributional data from throughout the Pleistocene.

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APPENDIX

Variable descriptions. (The standard deviation of 20 replicate measurements of one specimen [with remounting] is given in parentheses.)

Size Variables

Shell height (SHELLH): The distance (in mm) from base to apex of shell. In cases of extreme shell wear this variable was estimated on the basis of other specimens in the same sample. (0.38)

Shell width (SHELLW): The sum of the maximum distance perpendicular to the columellar axis on the right and left sides of the shell (in mm). Snails were mounted on 1-mm graph paper with coiling axis parallel to the y-axis of the paper. Width was measured on the shell image as the maximum delta x. (0.26)

Shell area (SHELLA): The area of the shell image calculated by Bioquant based on a manual tracing of the

shell image perimeter with the digitizer mouse (in mm²). (2.63)

Shell wall thickness (WALTHIK): The thickness of the shell wall, measured (with modified vernier calipers) just behind the first row of denticles on the body whorl, at approximately the second denticle from the adapical end (in mm). (0.09)

Shape Variables

Apical angle (ANGLERT): The acute angle measured in degrees between the columellar axis and the body whorl - penultimate whorl suture on the right edge of the shell (shell in standard position). (1.17)

Shell shape factor (SHELLSF): $4(\pi)$ (shell area)/(shell perimeter).² This variable is calculated by Bioquant (unitless). (0.04)

Height/width (HWDIV): The ratio of shell height to shell width (unitless). (0.03)

Apertural Variables

Aperture height (APTH): The distance along the columellar axis measured from the base of the siphonal canal to a point perpendicular to the suture line of the body whorl (in mm). (0.35)

Aperture width (APTW): The maximum width of the aperture along a line perpendicular to the columellar axis (in mm). (0.26)

Aperture height/aperture width (AHAWDIV): The ratio of aperture height to aperture width. (0.06)

Aperture area (APTAREA): The aperture area based on a manual tracing of the aperture image with the digitizer mouse (in mm²). (3.23)

Aperture shape factor (APTSF): $4(\pi)$ (aperture area)/(aperture perimeter)²; calculated by Bioquant: a measure of apertural shape (unitless). (0.04)

Aperture height/shell height (AHSHDIV): The ratio of aperture height to shell height; a measure of the relative size of the aperture. (0.01)

Miscellaneous

Shouldering (SHDR): The ratio of: (the traced distance along the right margin of the shell image from the apex to the adapical body whorl suture) divided by (the straight line distance connecting the same two points). This variable is a measure of the definition of shell shouldering. (0.14)

A New Genus and Species of Facelinidae (Opisthobranchia: Aeolidacea) from the Caribbean Sea

by

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Abstract. A new aeolid species has been found throughout the Caribbean Sea. It possesses the characteristics of the family Facelinidae and the subfamily Favorininae, but its reproductive structures differ from those of all other genera. This species is therefore placed in a new genus and compared to other genera in the subfamily.

INTRODUCTION

The tropical western Atlantic opisthobranch fauna is incompletely known, and relatively depauperate compared to the Indo-Pacific fauna. Nevertheless, almost 300 species have been described. The warm-water western Atlantic opisthobranch species are primarily endemic, but there are also many amphi-Atlantic species (EDMUNDS, 1968, 1977; JENSEN & CLARK, 1983; ORTEA *et al.*, 1988; TEMPLADO *et al.*, 1991). A number of Caribbean-Panamic species are recognized, and are thought to be representatives of a shared Pliocene fauna (MARCUS & MARCUS, 1967; BERTSCH, 1979; GOSLINER & WILLAN, 1991). There are also circumtropical representatives, possibly remnants of the Tethys Sea fauna.

Eveline and Ernst Marcus provided a sound basis for further opisthobranch research, summarized in their checklist of western Atlantic warm-water opisthobranchs (MARCUS, 1977). Since then, several synonymies have been made and at least 26 new species have been added (CLARK & GOETZFRIED, 1976; EDMUNDS & JUST, 1983; GOSLINER, 1989; GOSLINER & ARMES, 1984; GOSLINER & GHISELIN, 1987; GOSLINER & KUZIRIAN, 1990; HAMANN & FARMER, 1988; MARCUS, 1980, 1983; MEYER, 1977; NUTTALL, 1989; ORTEA & TEMPLADO, 1989; TEMPLADO *et al.*, 1987; THOMPSON, 1977, 1980). This paper describes a new aeolid genus and species belonging to the family Facelinidae.

SYSTEMATIC TREATMENT

ORDER AEOLIDACEA

SUPERFAMILY CLEIOPROCTA

FAMILY FACELINIDAE

SUBFAMILY FAVORININAE

Genus *Pauleo* Millen & Hamann, gen. nov.

Generic diagnosis: Rhinophores smooth or weakly lamellate. Cerata arranged on pedunculate arches with one or two rows per arch. Foot corners tentacular. Anus cleioproctic. Nephroproct interhepatic. Salivary glands simple. Oral glands absent. Jaw elongate, notched, and possessing a flange. Masticatory border with single row of denticles. Radula uniseriate with large, cuspidate rachidian teeth. Tooth shape triangular with many short denticles. Reproductive opening below anterior arch of first ceratal cluster. Reproductive system androdiaulic with proximal receptaculum seminis. Vas deferens non-prostatic. Penis with internal glands and proximal, non-glandular pouch containing vas deferens. Penial opening subterminal, unarmed.

Type species: *Pauleo jubatus* gen. & sp. nov., by original designation.

Pauleo jubatus Millen & Hamann, sp. nov.

(Figures 1–8)

Etymology: The numerous curly cerata that can bristle forward defensively suggested the generic and species names, which translate as “little lion’s mane.”

Material: Holotype: California Academy of Sciences CASIZ 077998, 1 specimen, 22 mm long. Specimen collected by J. Hamann on 24 May 1986; Grand Bahama, Bahamas, outer reef off Taino Beach (26°29'58"N, 78°36'45"W), at 20 m depth on a coral head on sandy substrate.

Paratypes: CASIZ 077294, 6 specimens, up to 28 mm long. Collected by T. Gosliner on 6 May 1991; S.W. Point, Grand Cayman, B.W.I., at 25 m depth on the gorgonian *Plexaurella dichotoma*.

United States National Museum of Natural History, USNM 860266, 1 specimen, 19 mm long. Specimen collected with the holotype.

Other collecting localities: Port Antonio, Jamaica, 2 specimens, largest 31 mm, at 13 m depth. Collected by J. Hamann, 23 August 1990. Discovery Bay, Jamaica, 10 specimens. Collected by J. Hamann on 14 December 1990, at 8 m depth, grazing on downed *Plexaurella dichotoma*.

Photographic records: Jackson Pt., Little Cayman, Cayman Islands. Photographed by Nancy Sefton, specimen on a coral head on a sandy bottom.

Bloody Bay, Little Cayman, photograph by Dr. Marc Chamberlain, November 1987, specimen on a patch reef at 10 m depth.

Lighthouse Reef, Belize, photograph by Thomas M. Sullivan, December 1984, of a specimen near the edge of a sandy reef at 12 m depth.

Eleuthera Island, Bahamas, photograph in COLIN (1978: 389), on a gorgonian at 20 m depth.

Guanaja, Honduras, 42 mm specimen photographed by J. Hamann, 8 August 1991, at 20 m on *Plexaurella*.

Systematic Description

External morphology: This translucent aeolid is suffused with pale orange on the head, tentacles, rhinophores, cerata, and dorsum. Underlying the orange suffusion is one of a variety of food-derived colors: orange, yellow, tan, pinkish beige, or blue gray. The animal has an elongate, slender, rounded body and a long trailing tail (Figure 1). A median, opaque white stripe extends along the head and down the full length of the body, narrowing between ceratal clusters. The line varies in width among specimens and may be interrupted. A small, opaque white crescentic patch is present on either side of the head just below the

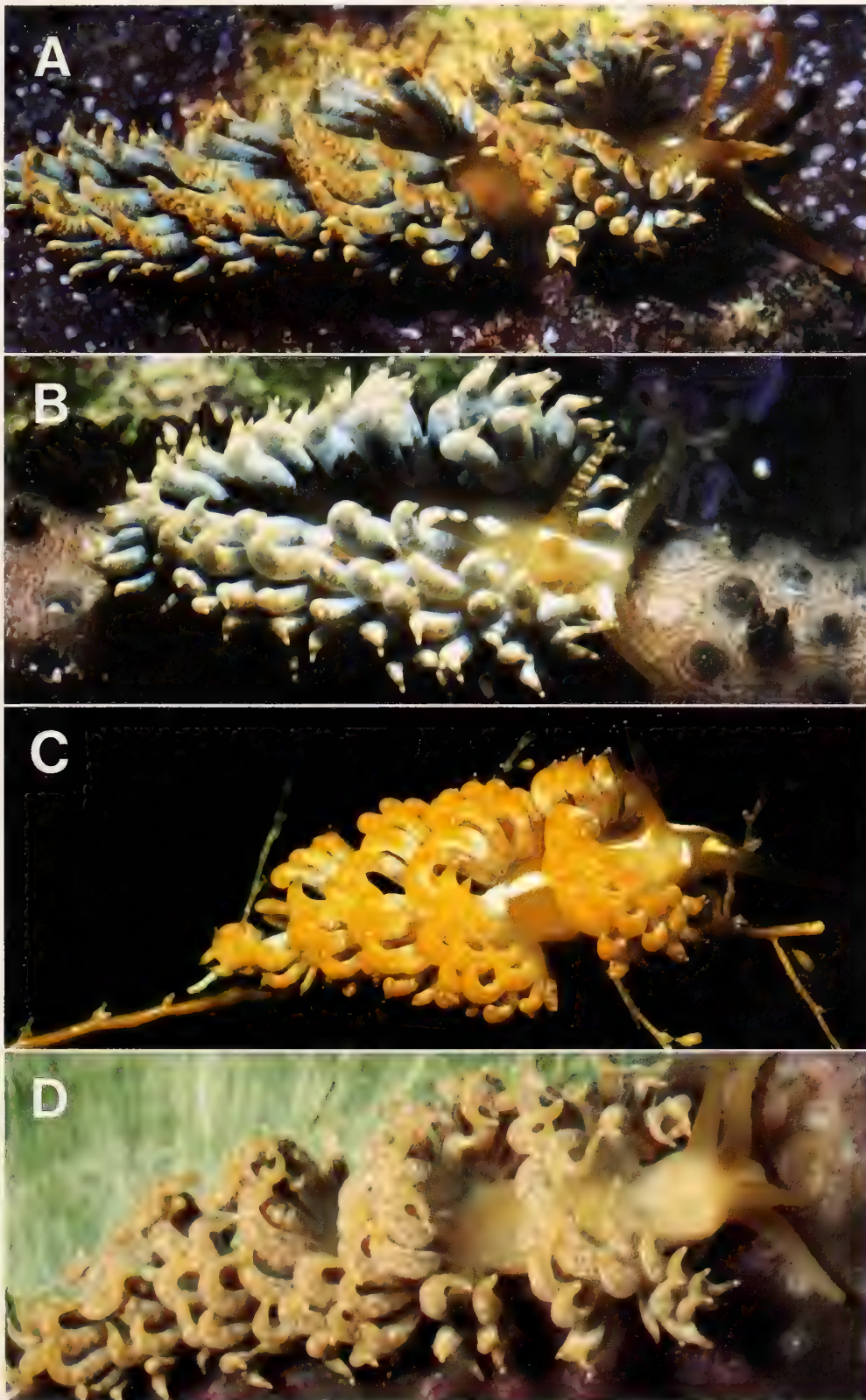
rhinophores. Live specimens measured up to 46 mm in length. The evenly tapered oral tentacles are slightly flattened. They are held anterolaterally and have a dorsal white line, wider near the base. The rhinophores are weakly lamellate with sloping bars of spicules overlaid with white pigment (Figure 1A, B) or smooth (Figure 1C, D). They are slender and evenly tapered to a fine tip. The rhinophores are much smaller in diameter and one-half the length of the oral tentacles. They end with a minute white tip. The head is rounded; the mouth a vertical slit (Figure 2). The foot has propodial tentacles that recurve inwardly and may be frosted with white coloration dorsally. The anterior margin of the foot and the propodial tentacles are bilabiate, with a well-developed groove that is wider medially. The foot is slender, with a central groove and a conspicuous flange that is one-third wider than the body itself. The long, slender tail has a slight medial keel.

The cerata arise from raised, arched cushions. There are up to eight clearly differentiated clusters of cerata per side (Figure 3). The pre-cardiac arches have a double row of cerata with alternating insertions and more cerata in the anteriormost limbs. The post-cardiac clusters are all in the form of arches with one row of cerata, except for the anterior limb of the first post-cardiac arch which has a double row. Within each arch, the cerata increase in size towards the center. The cerata are curved towards the midline of the body and are up to 6 mm in length in preserved specimens. When disturbed, the animal curls the cerata tips forward in a defensive posture (Figure 4). Each ceras is oblong in cross section and attached on its inner side. The translucent cerata are suffused with the food-derived color. There are small, opaque white tips on the cnidosacs followed by a translucent band through which the long cnidosacs can be seen. The distal one-third of each ceras has opaque white or bluish white spots on an orange ground. On most specimens, the middle one-third has a mottled white or bluish white band, which is more prominent on the anterior face of each ceras, on a background color that varies according to the food. The proximal one-third of each ceras lacks opaque white spots and shows the color of the digestive gland. The ceratal branches of the digestive gland are nodular. In each ceras a central branch with rounded lobules extends to the ceratal walls. These lobes are alveolar-like and have a honeycombed appearance. The cerata surfaces are smooth, but appear pustulate because numerous white pigment spots are located on the lobes. The long, functional cnidosac is lined with large glandular cells. The cerata are easily autotomized and move about for a short time after detachment.

The genital apertures are located below the anterior

Figure 1

Color variation in *Pauleo jubatus* gen. & sp. nov., Millen & Hamann. A. 32 mm specimen, Discovery Bay, Jamaica. B. 26 mm specimen, Discovery Bay, Jamaica. C. 30 mm specimen, Grand Bahama, Bahamas. D. 42 mm specimen on prey, *Plexaurella dichotoma*, Guanaja, Honduras.



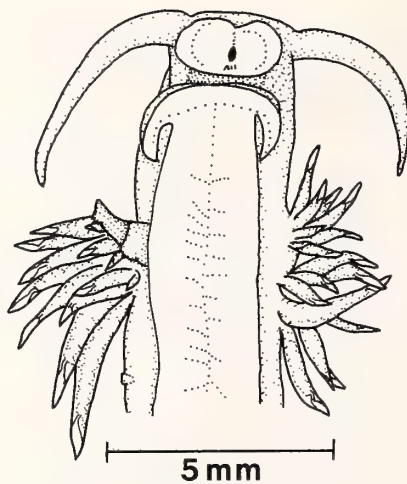


Figure 2

Pauleo jubatus, ventral view of head and foot.

limb of the first ceratal arch; the anal opening is posterior, within the second arch; and the renal pore is located in front of the second arch, in the interhepatic space (Figure 3).

Digestive system: The buccal mass has a circular, muscular, lip plate. The portion surrounding the mouth slit is convoluted and chitinized. The jaws (Figure 5) are covered by thin, unpigmented epithelium. They are pale golden brown in color, and rectangular, with a vertical flange for muscle attachment, and more posteriorly, a concave dorsal margin. The wing of each jaw is divided by a slight groove into an upper and a lower portion. The upper portion is smaller, lighter in color, and more convex than the lower portion (Figure 5A). The small masticatory process bears, near its tip, one row of approximately 10–18 small denticulations (Figure 5B).

The radular formula is 20–23 (0·1·0). The teeth have an elongate, bluntly pointed cusp with 9–14 small denticles on each steeply sloping side. A long pair of posterior limbs forms a narrow arch (Figure 6A). In some animals, in-

termediate denticles are present (Figure 7). In lateral view (Figure 6B), a prominent knob for articulation projects outward. The teeth are large: 200–460 μm long and 77–240 μm wide.

Oral glands are absent, and the small salivary glands are located dorsolaterally above the anterior portion of the stomach with long ducts inserting on the buccal bulb just above the buccal ganglia. The short, wide esophagus is lined with cuticle on the dorsal and lateral sides.

The S-shaped stomach has three parts. The forward portion is an elongate oval, curved slightly to the left, with longitudinal papillate striae. The smaller central portion arises dorsally and loops abruptly to the right through 90°, so its longitudinal striae are oriented transversely relative to the animal as a whole. Two anterior and one posterior hepatic ducts branch off this portion. The posterior portion of the stomach loops ventrally and to the left, narrowing gradually into the intestine. The latter runs longitudinally under the posterior hepatic duct and then abruptly bends dorsally and to the right to empty within the second ceratal arch. Each ceratal arch is served by one branch of the digestive gland.

Central nervous system: The oval cerebropleural ganglia are completely fused and connected together by a short wide commissure. The rhinophoral ganglia are on long stalks. The eyes are on very short stalks. Small statocysts lie behind the optic ganglia. The oval pedal ganglia are joined to the larger cerebropleural ganglia by short commissures, and to each other by a longer, wide, circumoesophageal commissure. The oval buccal ganglia lie beneath the oesophagus and are attached to each other by a short commissure.

Reproductive system (Figure 8): The ovotestis form large, round, grape-like lobules with the female ancini peripheral to the male ancini. There is a long thin ovotestis duct. The duct widens into a sausage-shaped hermaphroditic ampulla, which coils twice and then extends the length of the female gland mass, narrowing only slightly before bifurcating into a narrow oviduct and a wide vas deferens. The vas deferens is highly muscular until it enters the penis. The vas deferens does not have a distinct prostatic portion,

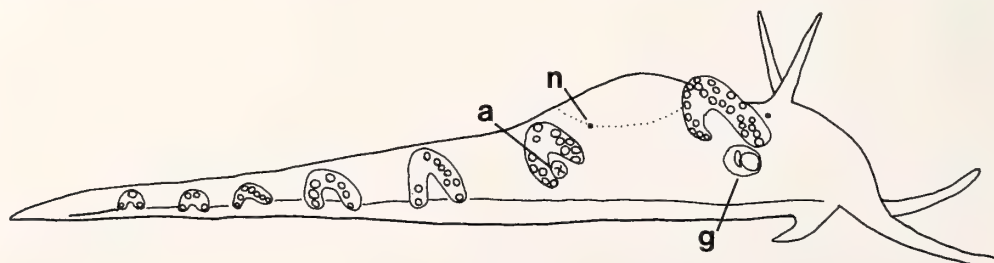


Figure 3

Right lateral view of *Pauleo jubatus* showing position of ceratal insertions. Key: a, anus; n, nephroproct; g, genital apertures.



Figure 4

Pauleo jubatus showing defensive bristling of the cerata with the cnidosacs pointing anteriorly.

although it is lined with a single layer of ciliated cuboidal cells, which are probably secretory in function. It loops and then enters a fibrous penial sac, which becomes wrinkled and deflated looking when the penis is everted. When the penis is withdrawn, the sac envelops the entire vas

deferens and upper portion of the penis. Inside the non-glandular penial sac, the muscular vas deferens enters the proximal portion of the penis. The penis is large, elongate, and flattened in cross section. In preserved specimens it is usually everted, with a small, slightly papillate sheath at its base. The vas deferens opens subterminally and the flattened tip is asymmetrical. The penis has highly muscular walls and an internal network of transverse muscle fibres, lacunae, and peripheral glandular cells which are larger on the posterior edge. The glandular cells become more numerous distally and occupy the entire tip of the penis beyond the opening of the vas deferens. No independent glandular opening was located and no internal duct entered the vas deferens.

There is a common atrium for the female gland mass and the vagina ventral to the posterior portion of the male aperture. The vagina forms the anterior face of the common

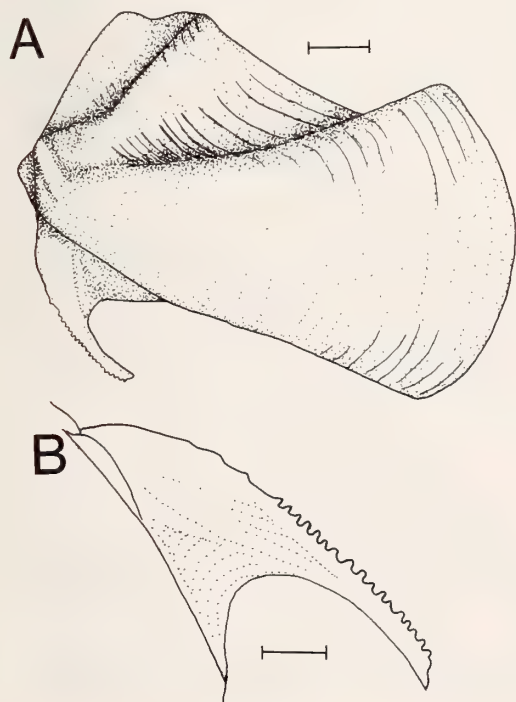


Figure 5

A. Outer view of right jaw plate of *Pauleo jubatus*. Scale bar = 0.1 mm. B. Masticatory margin of jaw plate showing denticles. Scale bar = 100 μ m.

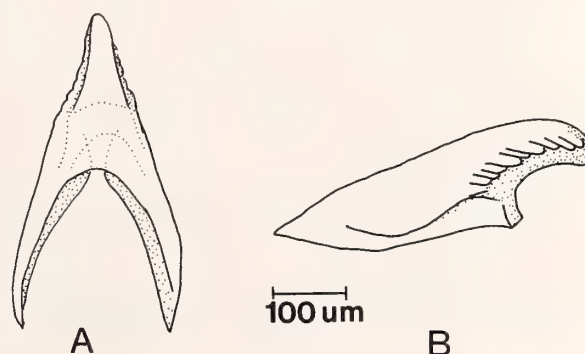


Figure 6

A. Dorsal view of a radular tooth of *Pauleo jubatus*. B. Lateral view of a worn radular tooth showing denticles.

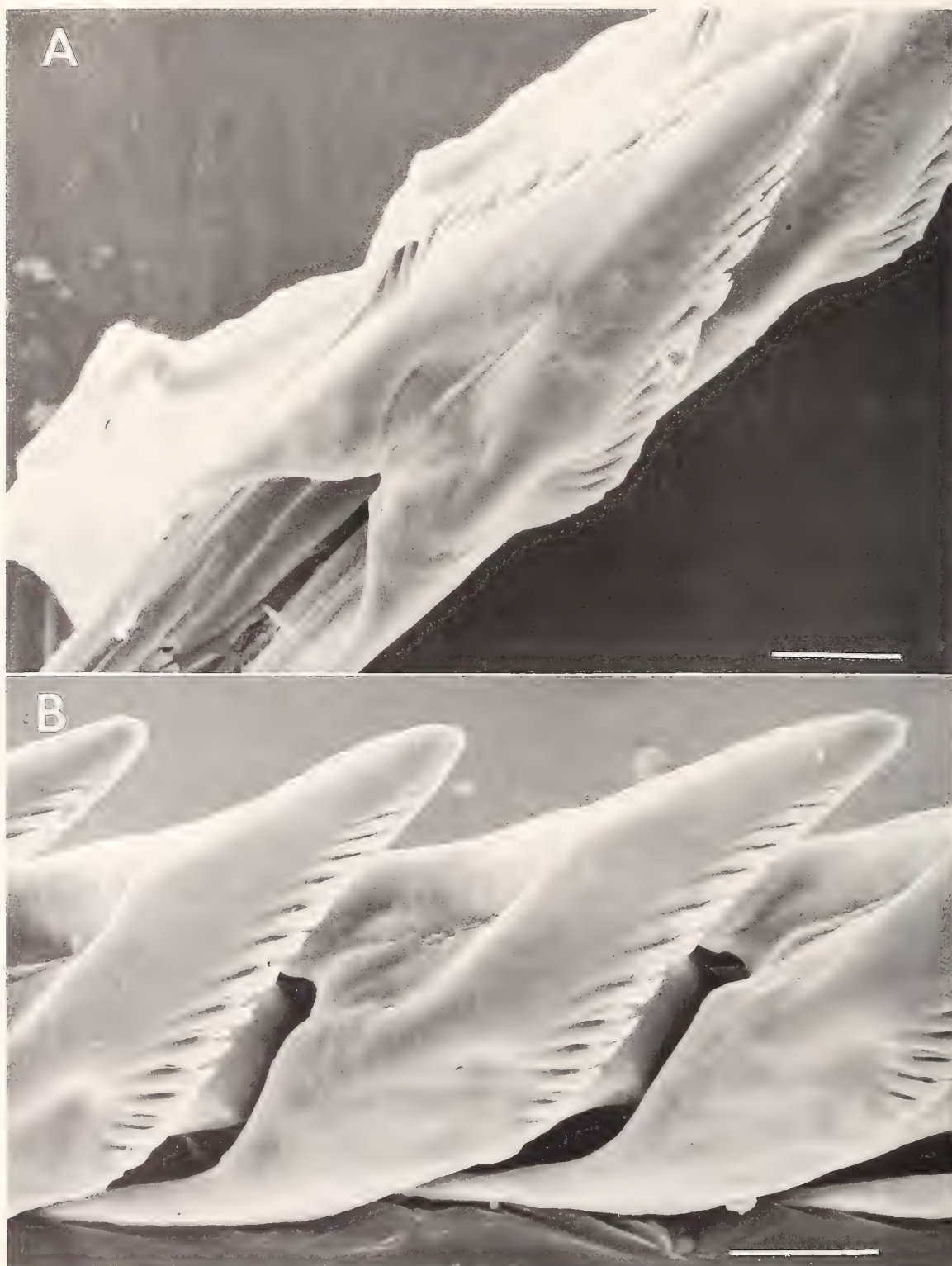


Figure 7

A. SEM view of the dorsal surface of an unused radular tooth of *Pauleo jubatus*. B. Dorsolateral view showing presence of intermediate denticles. Scale bar = 40 μm .

duct and continues as a tubular oviduct to the junction with the seminal receptacle. The semiserially arranged receptacle is elongate and irregularly lobate, with a short stalk. The long, tubular oviduct joins the hermaphroditic duct. The female gland mass is composed of a highly convoluted membrane gland, a small albumen gland, and a large mucous gland. The latter consists of two distinct lobes with the genital organs running down the groove between them.

Ecology: Little is known about this species. All specimens have been collected or photographed at night. They are usually found on the side of coral heads, on sandy bottoms, in 8–20 m of water. The darkest specimens, with a bluish gray cast to the body and dark blue-gray ceratal cores, were found feeding on the gorgonian *Plexaurella dichotoma*, as were some pale pinkish-tan specimens (Figure 1B, D). Functional nematocysts are present in the cnidosacs. The animal varies in color, which probably comes from a varied diet. Most dissected specimens had empty stomachs or fragments of soft polyps, but one specimen was full of opisthobranch eggs, suggesting that they are opportunistic feeders. Their spawn mass has not been seen.

DISCUSSION

Pauleo jubatus can be distinguished from all other aeolids in the Caribbean by its large body size and the defensive bristling of its cerata. *Phidiana lynceus*, which is not as large, has some orange coloration, but it can be easily distinguished because the cerata are in rows and have one or two white bands on each ceras.

The taxonomy of the aeolid family Facelinidae has recently undergone a number of rearrangements, summarized by EDMUNDS & JUST (1983) and WILLAN (1987). We favor their use of the family Facelinidae rather than the more all-encompassing Glaucidae proposed by MILLER (1974). The subfamily Favorininae is composed of genera whose cerata are arranged in arches, but this trait is considered polyphyletic so the subfamilies should probably be abandoned (EDMUNDS, 1970; WILLAN, 1987; GOSLINER, 1991). Generic placements are also rather unsatisfactory at present because most genera are separated almost entirely on the basis of different penial structures. These differences have been reviewed by MILLER (1974). Since then, however, three new genera have been added, *Hermosita* and *Bajaeolis* by GOSLINER & BEHRENS (1986) and *Anetarca* by GOSLINER (1991).

This new genus *Pauleo* has both pre- and post-cardiac ceratal clusters arranged in arches on elevated cushions, some of which bear double rows of cerata. A number of genera have the synapomorphy of cerata in arches rather than rows, which is the basis of the polyphyletic subfamily Favorininae. Raised ceratal cushions appear to be a derived state because none of the plesiomorphic reproductive characteristics (two bursae, serial receptaculum seminis) occur in these genera. This parallels the situation in the family

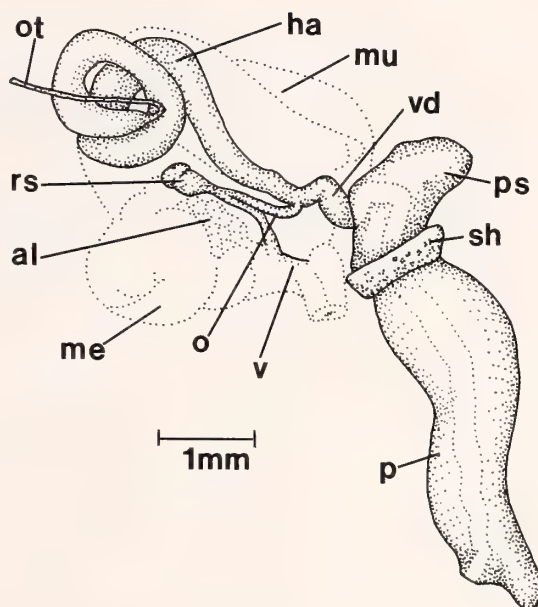


Figure 8

Reproductive system of *Pauleo jubatus* drawn using a camera lucida. Key: al, albumen gland; ha, hermaphroditic ampulla; me, membrane gland; mu, mucous gland; o, oviduct; ot, ovotestis duct; p, penis; ps, penial sac; rs, receptaculum seminis; sh, sheath; v, vagina; vd, vas deferens.

Flabellinidae (GOSLINER & GRIFFITHS, 1981). Multiple insertions of cerata on the arches are a plesiomorphic feature. All of the genera with raised, arch-shaped cushions are compared in Table 1, except for *Amanda*, *Godiva*, *Noumeaella*, and *Echinopssole*, which have apomorphic penial armature.

In addition to the arrangement of the cerata, other external features sometimes used for generic diagnosis are the shape of the rhinophores and the position of the genital openings. *Pauleo jubatus* has smooth or lamellate rhinophores and reproductive openings at the anterior limb of the first ceratal arch. These are both apomorphic conditions for the family (WILLAN, 1987) but because they occur in a number of genera in both subfamilies, they are not very helpful for comparative purposes.

Internally, the jaw structure of *Pauleo jubatus* has a number of apomorphies. It has an indented dorsal margin, a dorsal flange, and an upper and lower convex division separated by a groove. Each of these traits can be found in other genera from both subfamilies in the Facelinidae. However, only the genera *Dondice* Marcus, 1958, *Facalana* Bergh, 1888, and *Sakuraeolis* Baba & Hamatani, 1965, and the species "*Godiva*" *banyluensis* Portmann & Sandmeier, 1960, share all three apomorphies (Table 1). Their jaws all show an intermediate modification towards the extreme type found in the Glaucidae. The jaws of *Pauleo jubatus* are more elongate than all of the others, and differ from those of *Sakuraeolis* by having only one row of den-

Table 1

Genera of Favorininae having multiple rows of cerata on raised arch-shaped pedicles, and having no penial armature.

Genus	Rhinophores	Jaw		Masticatory border rows	Vas deferens	Penis
		Notch	Flange			
<i>Austraeolis</i>	annulate	—	+ (—)	single	proximal prostatic	circle of fleshy filaments
<i>Bajaeolis</i>	perfoliate	+	—	several	all prostatic	conical
<i>Dondice</i>	annulate	+	+	single	non-prostatic	basal gland, spiral groove, prostate gland
<i>Facalana</i>	perfoliate	+	+	single	?	leaflike expansion, fleshy glandular knobs
<i>Jason</i>	papillate	—	—	smooth	all prostatic	distal glands
<i>Pauleo</i>	smooth or perfoliate	+	+	single	non-prostatic	basal sac, internal glands
<i>Sakuraeolis</i>	smooth	+	+	several	all prostatic; 1 cell layer thick	fleshy lobes, stalked accessory gland
" <i>Godiva</i> " <i>banyluensis</i>	perfoliate	+	+	single	proximal prostatic	basal sac, conical penis

ticles and from those of "*Godiva*" *banyluensis* by lacking a flange-like guard.

Variations of the basic facelinid radula may be adaptations to different prey. The steep-sloping sides and many fine denticles on the radula of *Pauleo jubatus* are characteristic of the genus *Phyllodesmium* Ehrenberg, 1831. *Pauleo jubatus* was not placed in the genus *Phyllodesmium* because it has functional cnidosacs, the cerata are in arches on raised pads, and the large penis is highly muscular with internal glands. Most species of *Phyllodesmium* feed on alcyonacean octocorals and have symbiotic zooxanthellae, but *P. horridum* (Macnae, 1954) and *P. serratum* (Baba, 1949) feed on gorgonaceans (GOSLINER, 1987; RUDMAN, 1991).

Phyllodesmium horridum has teeth that are almost identical in shape to those of *Pauleo jubatus*, although they are proportionally much smaller—about one-half the size in similar sized animals. Externally, *Phyllodesmium horridum* differs from *Pauleo jubatus* due to its wider, more depressed shape, longer cerata, which are not borne on raised pads, and less tapering ceratal tips, rhinophores, and oral tentacles. Internally, the jaw of *Phyllodesmium horridum* is not as elongate, and its masticatory denticles are less developed. Both have a two-part jaw with a flange, but in *Phyllodesmium horridum* the two parts are not separated by a large notch and the smaller flange extends horizontally rather than vertically. The penial structures of the two species also differ greatly. *Phyllodesmium serratum* has a thin-walled, prostatic vas deferens, which terminates in a very tiny, muscular penis tip. The vas deferens of *Pauleo jubatus* is shorter, narrower, and muscular with a large, muscular penis containing internal glands.

Penial elaborations distinguish the various genera of Facelinidae. Table 1 compares species of the subfamily Favorininae that are most similar in ceratal arrangement to *Pauleo* and that do not have penial armature. The non-

glandular penial sac of *Pauleo* is found only in the species "*Godiva*" *banyluensis* (PORTMANN & SANDMEIER, 1960). This thoroughly described species has recently been removed from the genus *Godiva* because it lacks a penial spine (WILLAN, 1987). Previously it was removed from the original genus *Dondice* because it lacks a separate prostate in the penis and a basal penial gland (EDMUNDS, 1964). It is presently without a generic assignment. Although the sac around the vas deferens is like that in *Pauleo*, the rest of the male reproductive system is radically different. "*Godiva*" *banyluensis* has a long vas deferens that is prostatic before it enters the sac, but not after. Its conical penis does not contain internal glands. On the other hand, the elaborate stomach of this species, described by GARCÍA & GARCÍA (1984), resembles that of *Pauleo jubatus*.

Similar penial glands to those of *Pauleo jubatus* are found in the genera *Dondice*, *Jason*, and *Sakuraeolis*. *Jason* is separated on the basis of unusual jaw and radular morphology (MILLER, 1974) but *Dondice* and *Sakuraeolis* appear to be closely allied to *Pauleo*. The penises of both of these latter species are large, with interlacing musculature, blood lacunae, and internal glands. *Dondice occidentalis* (Engel, 1925) has an accessory penial gland at the base of the penis with a duct extending distally and emptying into the vas deferens either near the penis tip (MARCUS, 1958) or part way along the penis (EDMUNDS, 1964). It also has a prostate gland located inside the penis, which opens independently at its tip. This latter gland is similar to the penial gland found in *Pauleo*, although no separate duct could be found in histological sections. *Pauleo* lacks the basal penial gland of *Dondice*, although it has a non-glandular sac in the same position.

Sakuraeolis has a stalked accessory gland similar to the unstalked gland of *Dondice*. It does not have a separate prostate gland inside the penis, but the vas deferens is reported to be prostatic throughout its length, even though

it consists of only a single cell layer (BABA & HAMATANI, 1965). It appears that the vas deferens of *Pauleo* is similar. The penis of *Sakuraeolis* has fleshy flaps at the base of the penial gland, which are not found in either *Pauleo* or *Dondice*. The genital openings of both *Sakuraeolis* and *Dondice* are more posterior than those of *Pauleo*, and their teeth are different.

In conclusion, although *Pauleo* is clearly allied to a number of genera in the Favorininae, it possesses a unique combination of characteristics that do not comfortably fit into any other generic diagnosis. The newly created genus *Pauleo* presently contains only the type species, *Pauleo jubatus*.

ACKNOWLEDGMENTS

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A Warm Water Atlantic Synonymy, *Aphelodoris antillensis* Equals *Chromodoris bistellata* (Opisthobranchia: Gastropoda)

by

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Abstract. Study of the literature and comparison of specimens shows *Chromodoris bistellata* (Verrill, 1900), a species previously thought to be endemic to Bermuda, to be a junior synonym of *Aphelodoris antillensis* Bergh, 1879, a species known from throughout the Caribbean.

INTRODUCTION

Specimens collected over large geographic distances with minor differences in external appearance or internal anatomy have often given rise to two or more separate species names. Language barriers and incomplete descriptions make resolution difficult without later works to add to and append the original descriptions and/or a large body of collected material to work with.

Both *Chromodoris bistellata* (Verrill, 1900) and *Aphelodoris antillensis* Bergh, 1879, were recognized by later workers, who added important details and extended geographic ranges (see review of literature below).

From May 1983 until June 1988, I collected over 25 specimens of *Aphelodoris antillensis* from locations ranging from the Dominican Republic to Venezuela and including the type locality, the Virgin Islands. I became familiar with the range of morphological variation of *Aphelodoris antillensis* in the Caribbean, making it immediately apparent upon examination of *Chromodoris bistellata* from Bermuda that they were likely to be conspecific. That opportunity presented itself in July 1988 when I visited Dr. Kerry Clark and Dr. Duane DeFreese in Bermuda.

REVIEW OF LITERATURE

Aphelodoris antillensis Bergh, 1879

BERGH's (1879) detailed original description, in German, was done from preserved material collected in St. Thomas, Virgin Islands. Although comprehensive in content, there were no figures or description of live specimens.

MARCUS & MARCUS (1963) were the first to recognize Bergh's species in print. They reported conforming external features, and figured the dorsal view, head, and radula of one specimen from Curaçao. The inner denticle on the

innermost lateral tooth reported by Bergh was missing but not considered of systematic importance. Internal features were not presented owing to the condition of the preserved material. They later provided figures of the reproductive organs and recorded variations in the color patterns of a specimen collected in Florida (MARCUS & MARCUS, 1967). MARCUS & MARCUS (1970) also reported three specimens from Puerto Rico. MEYER (1977) recorded 10 specimens from Panamá and reported low tubercles on the notum that disappear upon preservation, accounting for their absence from earlier descriptions. THOMPSON (1980) reported two specimens from Jamaica. He noted the swimming/escape reaction also reported by GOSLINER (1987) for *Aphelodoris brunnea* Bergh, 1907. Thompson reported a yellow band on the notal border and confirmed the tubercles reported by Meyer. EDMUNDS & JUST (1985) collected three specimens in Barbados. They noted further minor variations in color and figured the spawn.

Chromodoris bistellata (Verrill, 1900)

VERRILL (1900) described *Doris bistellata* in 74 words. No internal features were reviewed and there were no figures. CLARK (1984) changed the genus to *Chromodoris* on the basis of the dentition, and figured the teeth. He also published the first photograph in *Marine Fauna and Flora of Bermuda* (JENSEN & CLARK, 1985).

TAXONOMIC TREATMENT

Material examined: *Aphelodoris antillensis*: Malmok, Aruba, 1 specimen, 20 mm, 2 m, December 1980; *Sa-

* Specimens deposited in the collection of the California Academy of Sciences.

maná, Dominican Republic, 6 specimens, 12–28 mm, 1 m, February 1984, CASIZ 075624, one specimen; La Parguera, Puerto Rico, 2 specimens, to 19 mm, 1 m, May 1984; Cayo Icacos, Puerto Rico, 1 specimen, 14 mm, 1 m, September 1984; Puerto Manglar, Culebra, 1 specimen, 1 m, December 1984; Lamshur Bay, U.S. Virgin Is., 6 specimens, to 29 mm, 1 m, March 1985; Green Key, British Virgin Is., 1 specimen, 17 mm, 1 m, June 1985; Indian Creek, Antigua, 1 specimen, 11 mm, 1 m, January 1986; Deshaies, Guadeloupe, 1 specimen, 19 mm, 2 m, January 1986; Trou Madame, Martinique, 1 specimen, 16 mm, 1 m, June 1986; Pt. Borghese, Martinique, 1 specimen, 18 mm, 7 m, June 1986; Piton Bay, St. Lucia, 1 specimen, 9 mm, 1 m October 1986; Bequia, St. Vincent, 1 specimen, 10 mm, 1 m, January 1987; Young Island, St. Vincent, 2 specimens, to 19 mm, January 1987; Clarkes Court Bay, Grenada, 1 specimen, 19 mm, 1 m, December 1987; *Chimana Grande, Venezuela, 2 specimens, 22 mm and 25 mm, 1 m, July 1989, CASIZ 075638; *Margarita, Venezuela, 1 specimen, 16 mm, 1 m, October 1989, CASIZ 075623; *Grand Cayman Island, British West Indies, 1 specimen, 18 mm, 1.5 m, May 1991, CASIZ 077289.

All collections were made by the author.

Chromodoris bistellata: *South Ferry Point, Bermuda, 3 specimens, 1 to 9 mm, 2 m, July 1988, collected by Duane DeFreese, CASIZ 075622.

Synonymy: Comparison of the specimens of *Chromodoris bistellata* from Bermuda with the previously described features of *Aphelodoris antillensis* and with a varied spectrum of preserved material of same confirm beyond reasonable doubt that they are in fact conspecific. There are no published or observed characteristics of *Chromodoris bistellata* that cannot be accommodated within the range of variability of *Aphelodoris antillensis*. Owing to the priority of Bergh's name, *C. bistellata* now becomes a junior synonym of *A. antillensis*.

External morphology: The base color is a translucent beige with widely varying amounts of yellow, brown, and white pigment, the yellow being totally absent in many individuals (Figure 1). The brown pigment spots are concentrated to form larger blotches on some individuals while others have an almost even density. Still others have such a dense concentration that they appear to have a brown base color. The yellow and white pigments are similarly sprinkled and/or concentrated over the dorsal surface in various degrees. Occasional specimens have brown and/or yellow dashes, formed by the pigment spots, perpendicular to the notal edge. Concentrations of white or brown

often form two more distinct blotches on the dorsum which, in the case of white, gave rise to the name *bistellata* or "two-starred" (Figure 2). The notal border can be rimmed in yellow but is generally unmarked. MEYER (1977) and MARCUS & MARCUS (1963) report an orange border. EDMUNDS & JUST (1985) report patches of wine-red color on the dorsal surface.

The body is 6 to 8 mm wide on a 20 mm individual and 4 mm high. Individuals tend to be plastic in shape, with some individuals at rest assuming a flatter, wider, body form. The dorsum is generally covered with low tubercles, independent of the color pattern, but these do not extend onto the notal margins. The body is very soft and smooth to the touch.

The narrow foot (2 to 4 mm on a 20 mm specimen) is well covered by the mantle and is the same width over most of its length. In front and back the foot is similarly rounded, with the back being slightly smaller. Only the posterior tip of the foot, which is similarly marked as the dorsum, is sometimes visible. Smaller brown and white pigment spots generally fleck the bottom of the foot and to a greater extent the hyponotum.

The mouth is round and grooved longitudinally. The tentacles, which BERGH (1879) reported as being very short and cut off, are typical in a live specimen (Figure 2) but shrunken in preserved material, as reported by MARCUS & MARCUS (1963). THOMPSON (1980) reported that although the tentacles were grooved or in-rolled in life their character was undetectable in his preserved material (Figure 3).

The rhinophores are typically shaped and strongly lamellate. A 20 mm specimen typically has 10–14 obliquely set lamellae sprinkled with brown and white pigment (Figure 4). BERGH (1879) reported 40 lamellae in his material from St. Thomas but my specimens (10–29 mm) from the type locality have 8–12 only. Other material, as well as all other reported data, support a much reduced number of lamellae. Bergh's specimen was 20 mm preserved and could well have been 40 mm or more in life, which could explain the high number of lamellae. The sheaths are smooth-rimmed and stand almost 1 mm high on a 20 mm specimen. Bergh reported that they are stiffened with thin brown calcified spicules (0.007–0.01 mm in cross section).

The simple branchial plume has five bipinnate gills that are sprinkled with brown and white pigment in concentrations parallel to the individual's body coloring. The gills are irregularly pinnate rather than featherlike. They also tend to have a more inflated center rib than most chromodorids. THOMPSON (1980) described them as thick and

Figure 1

Aphelodoris antillensis Bergh, 1879. A. 17 mm specimen from British Virgin Islands. B. 14 mm specimen from Puerto Rico. C. 20 mm specimen from Aruba. D. 16 mm specimen from Martinique. E. 19 mm specimen from St. Vincent. F. 25 mm specimen from Venezuela. G. 9 mm specimen from Bermuda. H. 25 mm specimen from Grand Cayman Island. Photographs by Jeff Hamann.



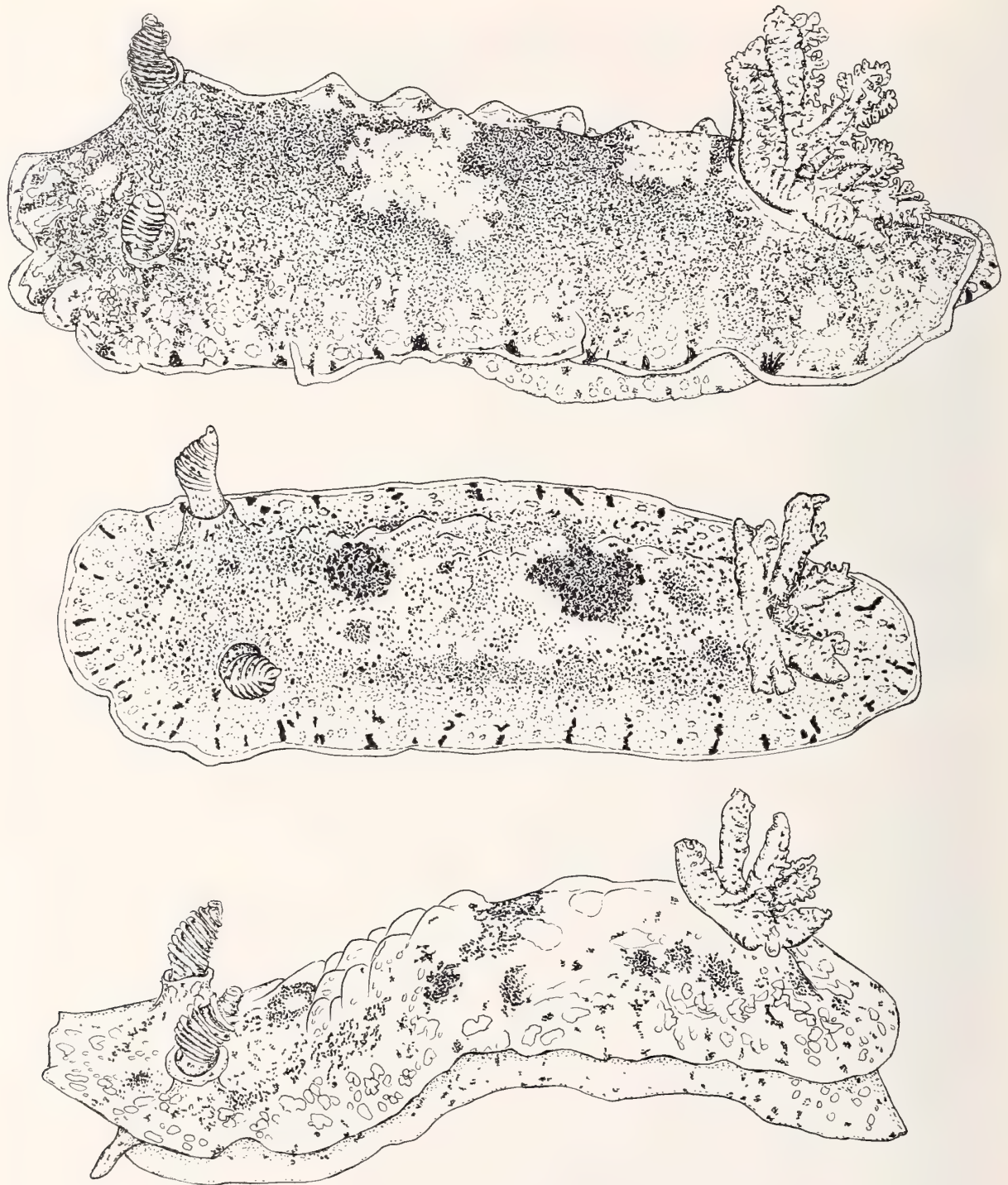


Figure 2

Aphelodoris antillensis. A. Concentrations of white pigment forming two distinct spots on the dorsum. B. Brown pigment forming larger blotches on the dorsum. C. Note typically chromodorid tentacles and thick and fleshy gills.

fleshy (Figure 2). The branchial plume can be withdrawn into a round branchial pit with a low smooth rim and no prominent markings. The plume is positioned farther back on the dorsum than on most chromodorids, 2–3 mm from

the posterior mantle edge on a 20 mm specimen. The short (0.5–1 mm) round anal papilla is in the center of the gill circlet.

EDMUNDS & JUST (1985) reported that the spawn rib-

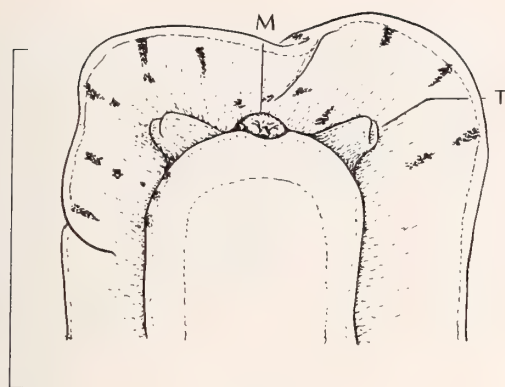


Figure 3

Head region of a preserved specimen of *Aphelodoris antillensis*. Key: T, contracted tentacles; M, mouth. Scale = 5 mm.

bon is two eggs thick and makes four and a half spiral turns. MARCUS & MARCUS (1970) recorded about 320 eggs in a spiral spawn from Puerto Rico.

In spite of the wide variations in colors, patterns, and body shape, specimens of *Aphelodoris antillensis* are easily recognized. The position of the branchial plume, softness of the body, and color variation within certain limits contribute to its widespread recognition. EDMUNDS & JUST (1985) found it unnecessary to examine the radula because "this species is easily recognized from its external features." Once some familiarity with the species is established the variations are quickly recognized.

Internal morphology: The jaw plates are constructed of a thick smooth cuticle. BERGH (1879) reported, and I confirm, that the radula is yellow. The radular formula varies widely with size and among individuals, with 30–52 rows and 30–68 teeth in a half row (Figure 5, Table 1). BERTSCH (1976) examined the variability of the radula in *Discodoris evelinae* and found 25–69 teeth per half row in 16–35 rows. Although he found positive correlations between size and both the number of teeth per row and the number of rows, he concluded that the number of teeth alone should not be used to establish the validity of a new species. The teeth are all simple hooks, except the outermost two or three,



Figure 4

Rhinophore of *Aphelodoris antillensis*. Scale = 3 mm.

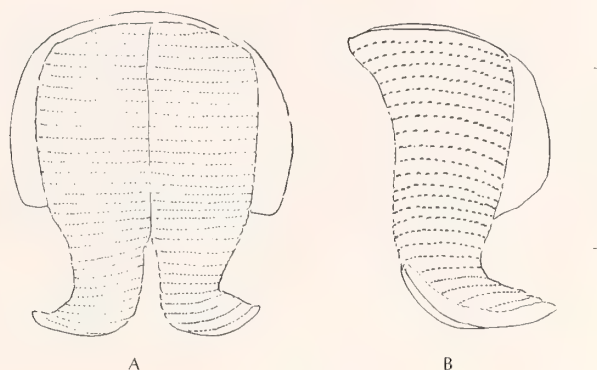


Figure 5

Radula of 16 mm *Aphelodoris antillensis* from Venezuela. A. Lateral view. B. Flattened dorsal view. Scale = 0.5 mm.

which can develop a projection on top of the hook. The middle teeth of each half row are the largest (Figure 6). BERGH (1879) reported that the innermost tooth had small denticles at its base. None of my specimens had any denticles and no other author has confirmed this characteristic. The large size of Bergh's specimen could explain their presence. MARCUS & MARCUS (1963) did not consider this absence to be of systematic significance because of the similar confirmed variability of denticles in *Discodoris pusae* Marcus, 1955.

The 28 mm specimen of *Aphelodoris antillensis* from Samaná, Dominican Republic, was dissected and compared to the 9 mm specimen from South Ferry Point. The reproductive systems were identical in arrangement and were in accordance with the description by MARCUS & MARCUS (1967) with the exception of the ampullary connection, which they showed near the oviduct. The important features also conformed to the description by BERGH (1879).

The genital mass is forward on the right side (Figure 7). A short sperm duct exits the female gland mass near the uterine duct. It connects to the prostate, which is composed of many sacs. The remaining vas deferens is con-

Table 1

Recorded radular variations in *Aphelodoris antillensis*.

Record	Radular formulas		
	Location	Size	Formula
BERGH, 1879	Virgin Islands	20 mm†	52 × 68.0-68
MARCUS, 1967	Florida	10 mm†	38 × 67.0-67
MARCUS, 1970	Puerto Rico	15 mm	42 × 66.0-66
THOMPSON, 1980	Jamaica	16 mm	36 × 58.0-58
MEYER, 1977	Panamá	?	35 × 55.0-55
MARCUS, 1963	Curaçao	15 mm	30 × 52.0-52
CLARK, 1984	Bermuda	5 mm†	30 × 36.0-36
Present study	Bermuda	9 mm	32 × 56.0-56
Present study	Venezuela	16 mm	30 × 43.0-43

† Preserved.

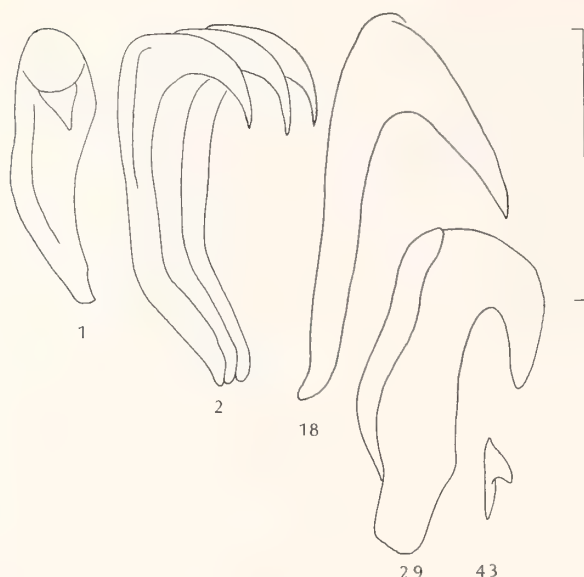


Figure 6

Teeth of *Aphelodoris antillensis* from Venezuela. Scale = 100 μ m.

voluted and about the same length as the prostatic portion. The penial sheath is muscular and the penis is unarmed.

The bulb-shaped vagina enters a spherical copulatory bursa of approximately equal size. The much longer distal vaginal duct then connects to the pear-shaped seminal receptacle, which is again about the same size. The uterine duct doubles back about half the length of the distal vaginal duct and then branches off to the female gland mass connecting near the oviduct. The long cylindrical ampulla enters the female gland mass at a location about half the diameter away from the uterine duct.

Discussion of the genus: *Aphelodoris antillensis* is the type species for the genus. Numerous later workers have recognized and/or used the genus, paradoxically all in southern temperate waters of Australia and South Africa (e.g., ODHNER, 1924; ELIOT, 1907; BURN, 1966; WILLAN & COLEMAN 1984; GOSLINER, 1987).

Aphelodoris was characterized by BERGH (1879) as very close to the Chromodoridae externally, but differing in the short hacked-off tentacles with a groove on the underside, the five plurally pinnate gill leaves, and the much smaller foot. Internally the rhinophores are stiffened with spicules, the jawplates are unarmed, the rachis is naked, the prostate is large, and the penis is unarmed.

I found the tentacles to be typically chromodorid in live material, and this opinion was voiced by MARCUS & MARCUS (1963) as well. Additionally, the gill is positioned farther back on the dorsum than on the typical chromodorid, and some species exhibit a head to tail swimming response to stimulation. The body is also soft and smooth to the touch.

BURN (1966) characterized the genus as follows: "glos-

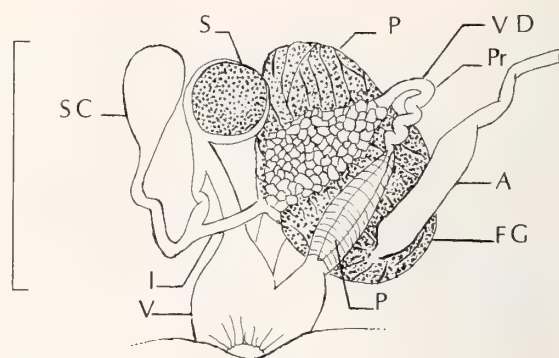


Figure 7

Reproductive system of *Aphelodoris antillensis*. Key: A, ampulla; FG, female gland mass; I, insemination duct; P, penis; Pr, prostatic portion of vas deferens; S, copulatory bursa; SC, seminal receptacle; V, vagina; VD, vas deferens. Scale = 2 mm.

sodoridiform" or high, slender, elongate body shape with usually narrow notal brim, smooth notum, high conical rhinophoral and branchial sheaths, laterally grooved oral tentacles, five-branched branchia, smooth labium, hook-shaped radular teeth without denticles, unarmed penial sheath, large prostatic part in male duct, and spermatheca and spermatocyst arranged serially (ODHNER, 1924) or semiserally.

ACKNOWLEDGMENTS

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A New Genus and Species of Polygyrid Land Snail (Gastropoda: Pulmonata) from Oregon

by

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Abstract. A new genus and species of polygyrid land snail, *Hochbergellus hirsutus*, is described from Sisters Rocks, Curry County, Oregon. *Hochbergellus* resembles *Vespericola* Pilsbry, 1939, but the penial chamber lacks a verge at the summit and has several internal pilasters that converge subapically to form a fleshy, anteriorly directed protuberance. The penial chamber lacks the prominent, paired dorsal pilasters found in *Cryptomastix* Pilsbry, 1939.

INTRODUCTION

The new taxon of land snail described here was collected during the course of a study by the authors (Roth & Miller, manuscripts in preparation) of the West American polygyrid land snail genus *Vespericola* Pilsbry, 1939. The species was first known to us from shells collected by the junior author in 1952 and subsequently by the late Robert R. Talmadge sometime before 1975. The junior author secured living specimens in 1991. On dissection, the species was found to lack the verge at the summit of the penial chamber that is diagnostic of *Vespericola*, but instead to bear longitudinal pilasters that fuse subapically into a fleshy, anteriorly directed protuberance. A consideration of anatomical relations among the new taxon, *Vespericola*, and *Cryptomastix* Pilsbry, 1939, leads us to propose a new genus for it.

MATERIALS AND METHODS

Shell height and diameter are vernier caliper measurements and exclude the expanded lip of mature shells. Whorls were counted by the method of PILSBRY (1939:xi, fig. B). The density of periostracal setae was estimated by counting the number of setae per square millimeter on the shoulder of the last 0.25 whorl of adult specimens, at 10× magnification under a dissecting microscope with an ocular reticle. Three counts were taken per specimen and the mean (to the nearest integer) recorded.

Specimens for dissection were prepared by the method of MILLER (1967). Snails were first drowned in water to insure expansion and relaxation, then heated to a temperature of 60°C, at which time the bodies could be pulled easily from the shells and dissected. The penis was slit longitudinally to expose the structures on the wall of the penial chamber.

Whole mounts of genitalia were prepared by the method of MILLER (1967): stained with hematoxylin, dehydrated and cleared in successive baths of ethanol and toluene, and mounted on slides with Permount mounting medium. Organ measurements were taken from mounted specimens. Anatomical drawings were made by projecting the image of the whole mount on paper with an overhead projector.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, senior author's collection, San Francisco, California; CAS, California Academy of Sciences; LACM, Los Angeles County Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; and USNM, National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

Family Polygyridae Pilsbry, 1895

Hochbergellus Roth & Miller, gen. nov.

Type species: *Hochbergellus hirsutus* sp. nov.

Polygyridae in which the shell is medium-sized, depressed-helicoid to conical, and narrowly umbilicate. The periostracum is matte-surfaced and bears rather sparsely set setae in diagonal rows. The base of the last 0.2 turn of the body whorl is compressed upward; a strong constriction is present behind the lip. A small parietal lamella is present. The lip is turned outward and reflected. No lamellae are present on the outer or basal lips, but the basal lip is thickened by a low callus. The epiphallus consists of a relatively thick upper section and a narrower lower section, markedly narrower than the apex of the penis. There is a completely enclosed, vestigial epiphallic caecum at the junction of epiphallus and vas deferens. A verge is absent. The upper cavity of the penis bears smooth



Explanation of Figures 1 to 3

Figures 1–3. *Hochbergellus hirsutus* Roth & Miller, gen. et sp. nov. Shell, holotype, SBMNH 35554, OREGON: Curry County: Sisters Rocks, ca. 3.8 km N of Euchre Creek at Ophir, W. B. Miller coll., 16 July 1991. Diameter 16.8 mm.

to papillose, longitudinal pilasters; four or more dorsal pilasters converge subapically to form a fleshy, anteriorly directed protuberance.

There are no diagnostic shell characters that distinguish *Hochbergellus* at the generic level from other polygyrid genera such as *Vespericola* and *Cryptomastix*.

The structure and organization of the reproductive system is much like that of *Vespericola*, except that *Vespericola* has a verge through which the seminal duct opens, either terminally or subterminally, into the penial chamber. A fleshy subapical protuberance in the upper penial chamber is not known to occur in *Vespericola*. The epiphallus is similar in *Hochbergellus* and *Vespericola* in consisting of a slender lower section tapering to a thicker upper section. In both genera there is a short, concealed epiphallal caecum at the junction of epiphallus and vas deferens. The spermathecal duct is relatively longer in *Hochbergellus* than in any *Vespericola* thus far examined.

The reproductive system is also similar to that of *Cryptomastix*, except that in *Cryptomastix* the upper part of the penial chamber bears a pair of large, contiguous, dorsal pilasters, with the seminal duct opening between their upper ends. The duct of the spermatheca is commonly thicker than in *Hochbergellus*.

Etymology: The genus is named for F. G. Hochberg, Jr., Curator of Invertebrate Zoology, Santa Barbara Museum of Natural History, who has keenly and consistently supported our studies of west American land mollusks.

Hochbergellus hirsutus Roth & Miller, sp. nov.

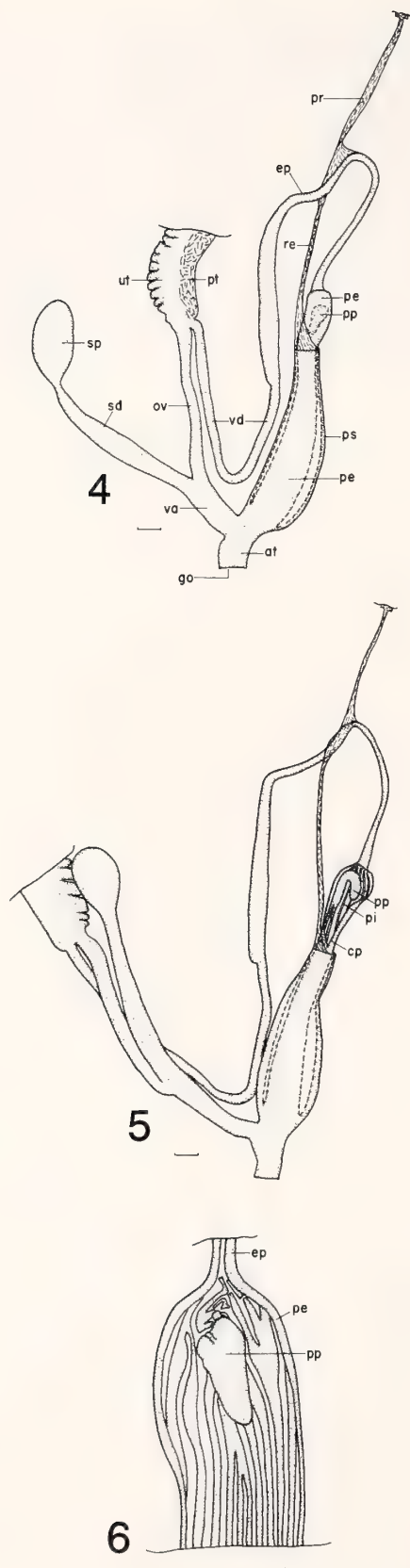
(Figures 1–6)

Diagnosis: A medium-sized polygyrid with depressed-helicoid to conical, narrowly umbilicate shell, 5.7–6.6 whorls, erect, distant periostracal setae, and usually a small parietal lamella. Penis elongate-conical, mostly enclosed in sheath; with subapical, anteriorly directed, fleshy protuberance formed by fusion of four or more longitudinal

pilasters; spermathecal duct long, slender, cylindrical; spermatheca ovate.

Description: Shell (Figures 1–3) medium-sized for the family, depressed-helicoid to conical, narrowly umbilicate, of 5.7–6.6 whorls; base inflated. Spire broadly conic, its sides straight or weakly convex; whorls flattened, suture weakly to moderately impressed. Embryonic whorls 1.5–1.8, sculptured with coarse, irregularly spaced papillae in diagonal trends and low, crowded, more or less granulose, radiating rugae, strongest below suture. Early teleoconch whorls with irregular, convex-forward retractive growth rugae and distant, erect or curved, acicular setae in protractive, descending rows; 2–3 setae/mm², approximately 0.7 mm long on spire and body whorl, broad at base, some with basal furcae pointing aperturally, many with finlike basal extension abaperturally. Periostracum between setae radially wrinkled, pebbly to scaly on first four whorls, smoother on whorls five and six, sometimes with a few raised spiral lirae on shoulder of body whorl. Periphery weakly subangulate, grading to rounded on last 0.5 whorl. Base regularly setose, setae smaller than on spire, extending into umbilicus. Last whorl not markedly descending, constricted behind lip. Aperture broadly auriculate, peristome shallowly concave in profile, oblique, at angle of about 30° to vertical; lip expanded and reflected, moderately thickened submarginally, most strongly turned backward at base. Inner lip reflected over narrow umbilicus. Basal lip thickened by low ridge of callus that may reach prominence of a tubercle on inner quadrant. Parietal callus granulose, free edge weakly convex, with shallow re-entrant below upper limb of peristome. Short, white, straight or upwardly convex parietal lamella usually present, set on upper third of parietal callus, somewhat back from line between upper and lower limbs of peristome. Shell tan, peristome white to pinkish tan.

Dimensions of holotype: Diameter (exclusive of expanded lip) 16.8 mm, height 11.1 mm, whorls 6.3.



Soft anatomy: The color of the living animal is tan along the foot, darker and grayer on the body-stalk. The mantle over the lung is clear buff, 10–40% maculated with black.

The holotype and nine paratypes were dissected.

The atrium (Figure 4) is of moderate length.

The penis is elongate-conical, somewhat bulbous at the summit, mostly enclosed anteriorly by a thin sheath adnate to the base. The penial retractor muscle is slender for most of its length, widening at its insertion on the epiphallus. A narrow strand of muscle, the “retentor,” extends from the penial retractor muscle at its attachment on the epiphallus to the summit of the penial sheath, from which other thin retentor fibers form connections with parts of the epiphallus and vas deferens. The sheathed part of the penis in the holotype is about 7.5 mm long; the protruding part is about 2.5 mm long. In the paratypes, the sheathed part varies from 6.0 to 8.0 mm (mean, 7.2 mm). The protruding part varies from 3.0 to 4.0 mm (mean, 3.6 mm). The mean ratio of protruding length to sheathed length is 0.5. There is a broad peduncular section of about 1.0 mm between the base of the sheath and the junction with the atrium.

The inner surface of the penis (Figures 5, 6) bears 12–14 long, parallel and anastomosing, longitudinal pilasters, varying from smooth-surfaced near the apex to distinctly papillose near the base. Near the apex, four or five pilasters fuse to form a thick, anteriorly directed fleshy protuberance. In one specimen this is a straight, cylindrical structure projecting anteriorly from near the apex of the penis for a length of 2.5 mm and a width of 0.6 mm. In all other specimens dissected, including the holotype, the structure forms a U-shaped, recurved, cylindrical appendage (Figure 6) attached to the dorsal wall of the penial chamber, with the recurved tip projecting anteriorly into the lumen for a length of about 1.2 mm. There is no verge. The epiphallic-seminal duct opens directly into the penial chamber at its apex.

The epiphallus consists of a relatively thick (0.8 mm

Explanation of Figures 4 to 6

Figures 4–6. *Hochbergellus hirsutus* Roth & Miller, gen. et sp. nov. Drawings made from projection of stained whole mounts. Scale line = 1 mm. Structures seen in transparency are shown by dotted lines. Figure 4. Anterior part of reproductive system, holotype, SBMNH 35554, OREGON: Curry County: Sisters Rocks, ca. 3.8 km N of Euchre Creek at Ophir, W. B. Miller coll., 16 July 1991. Figure 5. Anterior part of reproductive system with apical portion of penis opened to show fleshy protuberance and pilasters; paratype, SBMNH 35556, same locality data as above. Figure 6. Apical portion of penis opened and magnified to show parallel, anastomosing pilasters and fleshy penial protuberance; paratype, SBMNH 35557. Abbreviations: at, atrium; cp, cut edge of penis; ep, epiphallus; go, genital orifice; ov, oviduct; pe, penis; pi, pilaster; pp, penial protuberance; pr, penial retractor; ps, penial sheath; pt, prostate; re, retentor; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens.

diameter) upper section between the vas deferens and the penial retractor muscle, and a narrower tube between the penial retractor and the penis. There is a completely enclosed, vestigial epiphallid caecum at the junction of epiphallus and vas deferens.

The spermathecal duct is long, slender, and cylindrical, about 7.0 mm in length and 1.0 mm in width at its junction with the oviduct, narrowing to a 0.3 mm constriction at the base of the spermatheca. The spermatheca is ovate, about 3.5 mm long and 1.7 mm at its widest diameter in the holotype. In the dissected paratypes, the length varies from 2.5 to 3.5 mm and the width from 0.8 to 1.9 mm.

Type material: Holotype: SBMNH 35554 (shell and stained whole mount of genitalia). OREGON: Curry County: Sisters Rocks, ca. 3.8 km N of Euchre Creek at Ophir, W. B. Miller coll., 16 July 1991.

Paratypes: SBMNH 35556, 35557 (figured paratypes); SBMNH 35555 (30 unfigured paratypes); all from same locality as holotype. Additional paratypes deposited in ANSP, BR, CAS, LACM, and USNM.

Referred material (all, OREGON: Curry County): along trail from Ocean View Camp (2.3 km N of Euchre Creek at Ophir), W. B. Miller coll., 4 April 1952 (SBMNH). Sisters Rocks, between Port Orford and Gold Beach. R. R. Talmadge coll., before 1975; under logs (BR).

Remarks: In the material at hand, adult shell diameter ranges from 13.7 to 17.2 mm (mean of 54 specimens including holotype, 15.42 mm); height, 9.0 to 12.5 mm (\bar{x} = 10.48 mm); height-diameter ratio, 0.62 to 0.80 (\bar{x} = .680); number of whorls, 5.6 to 6.7 (\bar{x} = 6.06).

Hochbergellus hirsutus differs from other polygyrid species in southwestern Oregon in the reproductive system

characters specified above for the genus. At the type locality, *H. hirsutus* is sympatric with *Vespericola megasoma* (Pilsbry, 1928). The periostracal setae (2–3/mm²) are much sparser than those of *V. megasoma*. In addition, in *V. megasoma* the inner part of the basal lip is narrowed, then dilated backward so as to enclose the umbilicus from the left side.

For purposes of the American Fisheries Society list of the Scientific and Vernacular Names of Mollusks (TURGEON *et al.*, 1988), we propose the name "Sisters Hesperian."

Etymology: Latin, *hirsutus*, hairy.

ACKNOWLEDGMENTS

We are grateful to Ken Emberton for examining specimens and sharing with us his opinions on the systematic position of *Hochbergellus hirsutus*.

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Taxonomic Re-evaluation and Description of *Gari radiata* (Dunker in Philippi, 1845) (Bivalvia: Tellinoidea: Psammobiidae)

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Abstract. A re-examination of type material and literature has established the correct name for one rather common, tropical Indo-west Pacific species of psammobiid—*Gari* (*Psammobia*) *radiata* (Dunker in Philippi, 1845). Despite repeated misidentifications, the only true junior synonym is *Psammobia denikei* Martens, 1897. Resolution of the correct name required designation of lectotypes for *Psammobia virgata* Lamarck, 1818, *P. radiata* Dunker in Philippi, 1845, and *P. denikei* Martens, 1897. A description of *Gari radiata* is provided to distinguish it from the closely related, allopatric *G. livida* (Lamarck, 1818) and *G. convexa* (Reeve, 1857).

INTRODUCTION

I am currently revising the taxonomy of all the Indo-Pacific members of the bivalve family Psammobiidae. A monograph treating the 37 species from the Australian and New Zealand region is complete (WILLAN, in press) and research on the southeast Asian fauna is now under way. This contribution is intended as an adjunct to the former work, although the species dealt with here actually occurs within the geographical area encompassed by the latter work. This investigation has involved some research with literature on North Atlantic species because of a misidentification by LAMARCK (1818).

Gari radiata (Dunker in Philippi) has been known by no less than 20 different combinations of genus and species over the years (see synonymy below). Remarkably, nine of these combinations are misidentifications resulting from confusion with four other species. This paper confirms the current use of *Gari radiata* (Dunker in Philippi, 1845) as taxonomically correct.

On the basis of shell morphology *Gari radiata* belongs to the subgenus *Psammobia* Lamarck, 1818. It is a tropical species with a considerable resemblance to two temperate southern Pacific (*i.e.*, Australasian) species in the same subgenus—*G. livida* (Lamarck, 1818) (= *Psammotaea zonalis* Lamarck, 1818) and *G. convexa* (Reeve, 1857) (= *G. hodgei* Willan, 1980). The similarities between these three species have caused great taxonomic confusion. This paper provides a description to separate *G. radiata* from these

allopatric species as well as the sympatric *G. amethysta* (Wood). *Gari radiata* is briefly compared with *G. virgata* (Lamarck) to rectify LAMARCK's (1818) misidentification. I have not had the opportunity to study the anatomy of any of these species.

Abbreviations

- AMS—The Australian Museum, Sydney, Australia
BMNH—The Natural History Museum, London, England
c—Complete specimen, *i.e.*, both right and left valves present in the same lot though not necessarily joined (measurements of length for complete specimens in this contribution always relate to the right valve)
CAS—California Academy of Sciences, San Francisco, USA
h—Half valve (either right or left) only contained in lot
MNCN—Museo Nacional des Ciencias Naturales, Madrid, Spain
MHNG—Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN—Muséum National d'Histoire Naturelle, Paris, France
NHMW—Naturhistorisches Museum, Vienna, Austria
NMV—National Museum of Victoria, Melbourne, Australia
ZMA—Zoölogisch Museum, Universiteit van Amsterdam, Netherlands

ZMB—Museum für Naturkunde, Humboldt-Universität, Berlin, Germany

ZMUC—Zoologisk Museum, Copenhagen, Denmark

Gari (Psammobia) radiata (Dunker in Philippi, 1845)

(Figures 1–12, 19)

Synonymy

Solen sp.: BRUGUIÈRE, 1797:pl. 227, fig. 5.

Psammobia radiata DUNKER IN PHILIPPI, 1845:194, pl. 2, fig. 5; DUNKER, 1882:187; PILSBRY, 1895:122; MARTENS, 1897:244, no. 7; HIDALGO, 1903:85; HABE, 1977:220; HABE, 1981:139.

Psammobia amethystus Wood: REEVE, 1856, *Psammobia* pl. 3, species 19 (misidentification, not *Solen amethystus* Wood, 1815).

Psammobia compta Deshayes: REEVE, 1857, *Psammobia* pl. 4, species 24 (misidentification, not *Psammobia compta* Deshayes, 1855).

Gari compta (Deshayes): TRYON, 1868:73, *Gari* species 8; BERTIN, 1880:110, no. 34 (misidentification, not *Psammobia compta* Deshayes, 1855).

Gari radiata (Dunker): TRYON, 1868:75, *Gari* species 31; BERTIN, 1880:122, no. 67; KURODA & HABE, 1952:20.

Gari (Psammocola) virgata (Lamarck): BERTIN, 1880:125, no. 80 (misidentification, not *Psammobia virgata* Lamarck, 1818).

Psammobia zonalis (Lamarck): E. A. SMITH, 1885:94 (in part); LYNGE, 1909:211 (in part) (misidentification, not *Psammotaea zonalis* Lamarck, 1818).

Psammobia (Gari) amethystina (sic = error pro. *amethystus*) Reeve (sic = error pro. Wood): PAETEL, 1890:39 (misidentification, not *Solen amethystus* Wood, 1815).

Psammobia (Psammocola) radiata Dunker: PAETEL, 1890:40; SHIKAMA, 1964:85; SCARLATO, 1965:51, pl. 2, fig. 5.

Psammobia denikei MARTENS, 1897:243, *Psammobia* no. 5 (new synonym).

Psammobia compta Deshayes: HIDALGO, 1903:88, no. 165 (misidentification, not *Psammobia compta* Deshayes, 1855).

Hiatula (Psammotaea) radiata (Dunker): STANDEN & LEICESTER, 1906:294.

Psammobia virgata Lamarck: LAMY, 1914:22 (misidentification, not *Psammobia virgata* Lamarck, 1818).

Gari (Gari) radiata (Philippi) (sic = error pro. Dunker in Philippi): PRASHAD, 1932:300.

Psammocola radiata (Dunker): HABE, 1952:204; KIRA, 1959:153, pl. 59, fig. 2; KIRA, 1962:170, pl. 60, fig. 2; HABE & KIKUCHI, 1960:24.

Gari sibogai Prashad: HABE, 1964:197, pl. 61, fig. 3 (misidentification, not *Gari sibogai* Prashad, 1932).

Gari (Psammocola) radiata (Philippi) (sic = error pro. Dunker in Philippi): SCARLATO, 1965:51, no. 6, pl. 2, fig. 5. *Gobraeus radiatus* (Dunker): KURODA *et al.*, 1971:43 (English part), pl. 97, fig. 10.

Psammobia rabiata (sic = error pro. *radiata* Dunker): HIGO, 1973:368, no. 1150.

Gari (Psammobia) radiata (Dunker): MATSUMOTO, 1979:109, no. 1845.

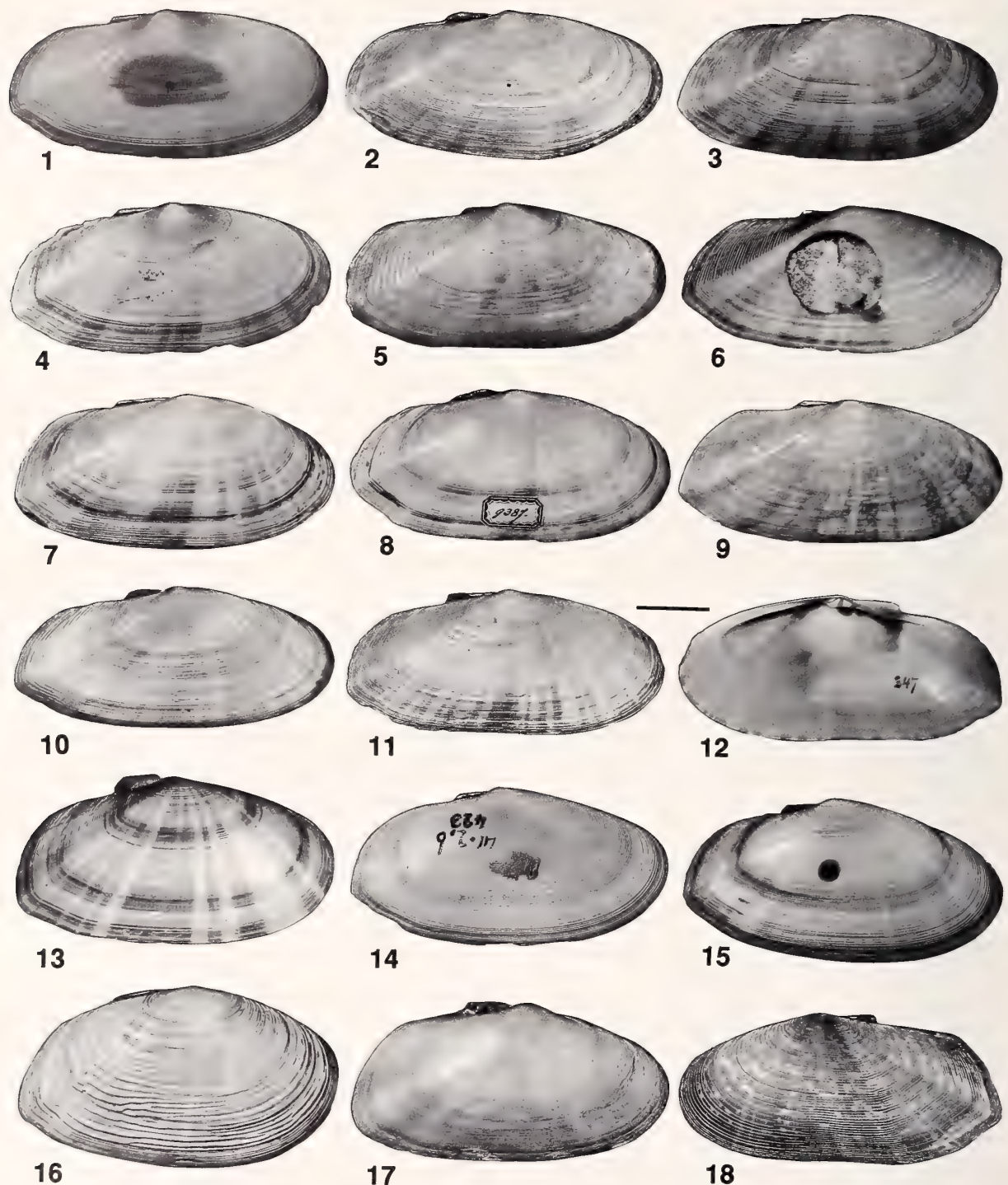
Like all the common Indo-Pacific psammobiids, the species forming the subject of this investigation has had a complicated taxonomic history. Its first appearance was in

BRUGUIÈRE's (1797) *Tableau Encyclopédique et Méthodique de Trois Règnes de la Nature*, but no name was supplied for the figured specimen. That shell must have come from Bruguière's own collection and it cannot now be located in MNHN. LAMARCK (1818:512) listed the Bruguière figure in the synonymy of his new species *Psammobia virgata*. However, judging by the two syntypes of *P. virgata* Lamarck (Figure 17) which are in the Lamarck collection, MHNG, *P. virgata* is the North Atlantic species generally assigned to *Gari intermedia* (Deshayes, 1855). This same conclusion was reached by DESHAYES & MILNE-EDWARDS (1835) and CHENU (1862). (Obviously Deshayes changed his mind over the identity of *P. virgata* Lamarck, because earlier he had informed Hanley that it was the same as *P. fervensis* Gmelin [HANLEY, 1843:59].) Therefore, Bruguière's figured specimen was neither a syntype, nor from the same geographical region, nor indeed even the same species as the syntypes of *P. virgata* Lamarck. To resolve the matter finally, I hereby designate as lectotype of *Psammobia virgata* Lamarck the larger syntype (probably the shell figured by CHENU, 1862) (complete specimen—48.6 mm) in MHNG (1083/10/1). The lectotype is illustrated here in Figure 17. The smaller specimen in MHNG (38.2 mm, 1083/10/2) becomes a paralectotype. This action fixes *P. virgata* Lamarck as the senior synonym of both *P. costata* Hanley, 1842, and *P. intermedia* Deshayes, 1855.

In the Lamarck collection, MNHN, there are two complete shells (51.1, 48.5 mm) of the species under consideration (Figure 1). On the back of the wooden tablet to which they both remain glued is the label "*psammobie vergatae Psammobia virgata* var. [c]" written by Lamarck, and on the front is the annotation "*Types de Lamarck*" written by some person subsequent to Lamarck (possibly Bertin). As LAMY (1914:4) observed, Lamarck never mentioned a variety "c," nor does his description of *Psammobia virgata* correspond with these shells, so they cannot be considered type material.

DUNKER (1845) gave a thorough description as well as excellent figures of the present species under the new name of *Psammobia radiata*. Authorship must be attributed to Dunker in Philippi, because on the title page of Philippi's *Abbildungen und Beichreibungen neuer oder wenig gettanner Conchylien 1* is the statement that the work contains contributions by Anton, van Dem Busch, Dunker, Jonas, Koch, Pfeiffer, and Troschel. Further, the letters "Dkr" (= Dunker) appear on page 194 in bold type beside the first introduction of the name *Psammobia radiata*.

Reeve figured two shells of *Gari radiata* in his *Conchologia Iconica*. The first (REEVE, 1856, *Psammobia* species 19) was erroneously called *Psammobia amethystus*. The actual shell (Figure 2) is in BMNH. The second (REEVE, 1857, *Psammobia* species 24) was called *Psammobia compta* Deshayes and localized from "Catbalonga, Island of Samar, Philippines." However, the type locality cited by DESHAYES (1855—publication date authenticated by DUNCAN, 1937) for *P. compta* was "Van Diemen's Land" (*i.e.*, Tasmania).



Explanation of Figures 1 to 18

Figures 1 to 12. *Gari radiata* (Dunker in Philippi). Figure 1. Smaller of two shells labelled *Psammobia virgata* var. [c] in Lamarck collection, MNHN, 48.5 mm, unknown locality. Figure 2. Specimen figured as "*Psammobia amethystus*" by REEVE (1856), 66.6 mm, Ceylon, BMNH 1964018. Figure 3. Specimen figured as "*Psammobia compta* Deshayes" by REEVE (1857), 50.7 mm, Catbalonga, Island of Samar, Philippines, BMNH 1984294/1. Figure 4. *Psammobia radiata* Dunker in Philippi, lectotype (selected herein), 48.4 mm, Amboina, Java, ZMB 25463. Figure 5. *Psammobia denikei* Martens, lectotype (selected herein), 21.7 mm, Makassar, ZMB 25069. Figure 6. 41.6 mm, unknown locality, Deshayes collection, MNHN. Figure 7. 47.9 mm, Manila, Luzon Island, Philippine Islands,

The syntypic series of *P. compta* Deshayes, including the shell figured under that name by Reeve, is in BMNH. The series consists of two *G. compta* (Lamarck) (35.4, 27.4 mm) and one *G. radiata* (52.4 mm). For conformity with DESHAYES' (1855) description, and particularly because of his type locality for *P. compta*, I have selected the 35.4 mm specimen of *G. compta* (BMNH 1841.2.6.423) (Figure 14) as lectotype (WILLAN, in press), and thereby relegated *G. compta* as a junior synonym of *G. livida* (Lamarck).

BERTIN (1880) wrongly construed the two specimens labelled *Psammobia virgata* var. [c] (now in MNHN) as types and, following REEVE's (1856) first illustration, reached the erroneous conclusion that *Psammobia virgata* Lamarck should replace *P. amethystus* of Reeve (not Wood, 1815). The fact that DAUTZENBERG & FISCHER (1913, 1914) made no mention of *Psammobia virgata* in their otherwise complete account of Lamarck's psammobiids suggests they realized the two specimens labelled var. [c] in MNHN were not types. LAMY (1914) simply noted the existence of these two shells, and reached no conclusion on their status.

E. A. SMITH (1885:94) synonymized *Psammobia radiata* with *Psammotaea zonalis* Lamarck on the basis of coloration, concluding: "It [*Psammobia zonalis* (Lamarck)] varies somewhat in painting, some forms being more rayed than others." LYNGE (1909) followed E. A. Smith. PRASHAD (1932) disputed E. A. Smith's union of *P. radiata* and *P. zonalis*, and he used the name *Gari radiata* (wrongly attributed to Philippi) for specimens collected on the *Siboga* Expedition. Following Prashad, the name *Gari radiata* (Dunker) has subsequently been adopted by most Asian workers except HABE (1964) who incorrectly used *G. sibogai* Prashad.

DESHAYES (1855) was apparently unaware of Dunker's *Psammobia radiata* when he described *Capsa* (*Capsella*) *radiata*, or if he did know Philippi's *Abbiungen*, he could not have conceived that *P. radiata* and *G. radiata* might be placed in the same genus one day. Now, in fact, both taxa are in *Gari*, and although *G. radiata* Deshayes (Figure 17) is the secondary homonym, there is no need to replace it

because that name falls as a junior synonym of *G. elongata* (Lamarck, 1818) (ICZN, 1985:Article 60a).

Psammobia denikei Martens (Figure 5) is based on two juvenile shells of the species under consideration. As such, that name is the one and only true junior synonym of *P. radiata* Dunker in Philippi.

The following sections (Types through Material Examined) all relate specifically to *Gari radiata* (Dunker in Philippi, 1845). In the descriptive section, terminology related to shell morphology follows COX (1969:N39-N58) for an equivalve bivalve except I have substituted umbo (plural, umbones) for beak.

Types

Psammobia radiata Dunker in Philippi: Lectotype, here designated (figured syntype, complete specimen—48.4 mm) in ZMB (Dunker coll. 25463); figured by DUNKER IN PHILIPPI, 1845, *Psammobia* pl. 2, fig. 5; illustrated here in Figure 4. Paralectotype (complete specimen—46.7 mm) in ZMB (25463). Type locality Amboina, Java.

Psammobia denikei Martens: Lectotype, here designated (larger, figured syntype, complete specimen—21.7 mm) in ZMB (25069); figured by MARTENS, 1897:pl. 10, fig. 25; illustrated here in Figure 5. Paralectotype (complete specimen—17.0 mm) in ZMB (25069). Type locality Makassar.

Historically Important Figured Specimens

Specimen figured as *Psammobia amethystus* by REEVE (1856) (complete specimen—66.6 mm) in BMNH (1964018); illustrated here in Figure 2. Locality Ceylon.

Specimen figured as *Psammobia compta* Deshayes by REEVE (1857) (complete specimen—50.7 mm) in BMNH (1984294/1); illustrated here in Figure 3. Locality Catbalonga, Island of Samar, Philippines.

Description

Maximum length 60 mm. Shell moderately thick, elongate; greatest width at level of umbones; nearly equilateral at all stages of growth, although slightly longer posteriorly; moderately inflated; anterior end rounded; ventral margin

CAS. Figure 8. 53.7 mm, unknown locality, NHMW G9387. Figure 9. 37.1 mm, 9–16 m, off Cape Liant and Mesam Island, Mellem, Thailand, ZMUC. Figure 10. 46.0 mm, Japan, MNHN. Figures 11 (exterior) and 12 (interior). 53.5 mm, unknown locality, NHMW 347.

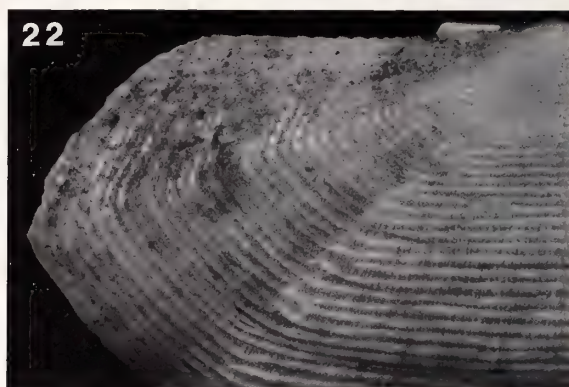
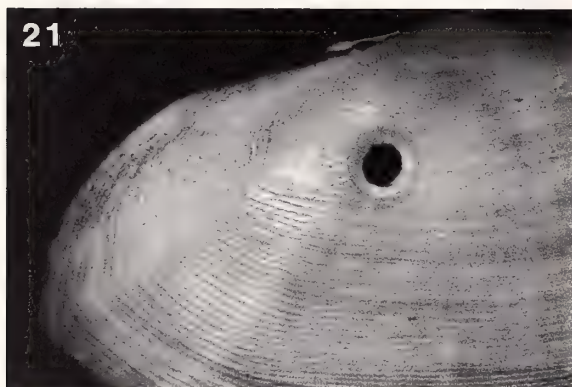
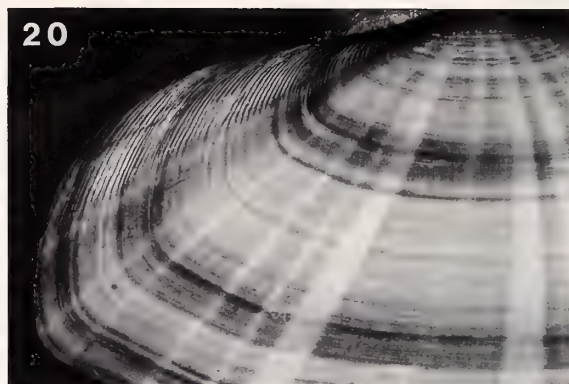
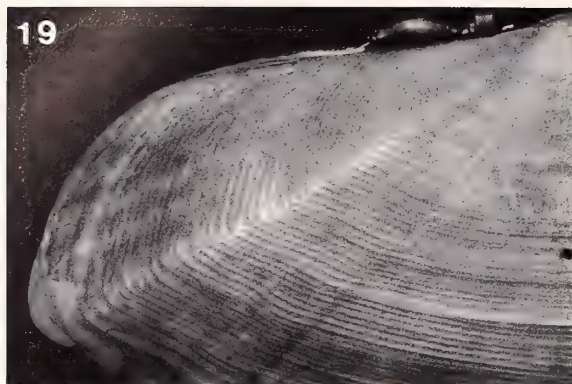
Figure 13. *Gari convexa* (Reeve). 54.2 mm, Smokehouse Bay, Port Fitzroy, Great Barrier Island, New Zealand, Willan collection.

Figures 14 and 15. *Gari livida* (Lamarck). Figure 14. *Psammobia compta* Deshayes, lectotype (selected by WILLAN, in press), 35.5 mm, Tasmania, BMNH 1841.2.6.423. Figure 15. 36.0 mm, Southport, southern Tasmania, WAM 1051-70.

Figure 16. *Gari virgata* (Lamarck). *Psammobia virgata* Lamarck, lectotype (selected herein), 48.6 mm, "Indian Ocean," Lamarck collection, MHNG 1083/10/1.

Figure 17. *Gari elongata* (Lamarck). *Capsa* (*Capsella*) *radiata* Deshayes, lectotype, 36.2 mm, Philippine Islands, BMNH 1984267/1.

Figure 18. *Gari amethysta* (Wood). 50.5 mm, Manila, Luzon Island, Philippine Islands, MNHN.



Explanation of Figures 19 to 22

Detail of sculpture on posterior slope of right valve of *Gari* (*Psammobia*) species. Figure 19. *G. radiata* (Dunker in Philippi), 66.6 mm, Ceylon, BMNH 1964018. Figure 20. *G. convexa* (Reeve), 54.2 mm, Smokehouse Bay, Port Fitzroy, Great Barrier Island, New Zealand, Willan collection. Figure 21. *G. livida* (Lamarck), 39.4 mm, unknown locality, Australia, BMNH 1985182/1. Figure 22. *G. amethysta* (Wood), 28.8 mm, Philippine Islands, NMV.

almost straight; posterior end narrower than anterior end, subacute, with distinct angle at termination of posterior ridge; equivalve (left valve slightly flatter in large adults); commissure at junction of valves' ventral margins straight (sometimes weakly sinuous); moderate anterior and small posterior gapes. Surface of both valves highly polished, smooth, anterior and middle sections sculptured only with broad, irregular, concentric growth furrows that become more incised near anterodorsal margin. Right valve with a ridge extending from umbo to posterior extremity; numerous, fine, raised, concentric striae always extend without interruption from posterodorsal margin to this ridge, and, in some specimens, striae cross ridge to become irregular, flattened lamellae on posteroventral area of central section; weak ridge but no striae in corresponding position on left valve. Exterior covered with a very thin, dehiscent, pale greenish-brown periostracum. Hinge plate narrow, moderately elongate; nymph moderately thick, high. Right valve with two cardinal teeth, each oblique and of approximately equal strength, the anterior one weakly bifid, the rear one strongly so, diverging from each other at 60°.

Left valve with single, weakly bifid anterior cardinal tooth; rear cardinal tooth represented merely by a low lamella on hinge plate, sloping at 65° behind anterior cardinal tooth; distinct, small lunular projection (stronger than posterior cardinal) bearing a microscopic lunular ligament also present on left valve. Pallial sinus deep (reaching halfway between hinge plate and rear margin of anterior adductor scar), broad, U-shaped; upper limb gradually descending; anterior margin rounded (more broadly in right valve); lower limb confluent with pallial line for most of its length; ventral extremity of pallial line straight, reaching level with rear of posterior adductor scar (Figure 12). Single, irregularly shaped pedal retractor scar present dorsally in front of hinge plate. Color of exterior bluish lilac, often faintly marbled, interrupted by numerous, either wide or narrow, reddish rays that emanate from white umbones; rays maintain coloration across shell; rays not symmetrical on right and left valves; central section of interior with purplish glaze and darker, brown-violet patches on either side of white umbonal area; posteriorly, brown-violet color extends onto nymph; reddish rays

prominent at ventral margin, which is white through lack of overlying purplish glaze.

Remarks

Gari radiata is closest to *G. convexa* (Reeve) (= *G. hodgei* Willan, synonymy discussed by WILLAN, in press) and *G. livida* (Lamarck). However, there are several characters that consistently separate these three allopatric species. (*G. radiata* was not compared with *G. convexa* in an earlier paper [WILLAN, 1980].) Compared with *G. radiata*, *G. convexa* (Figures 13, 20) from New Zealand is larger (to 85 mm), heavier, markedly inequilateral when adult and less elongate, the anterodorsal margin descends more steeply, the posterior margin is relatively broader (but still angulate), the right valve is more inflated, and the left valve is flatter resulting in a more sinuous commissure, the posterior ridge on the right valve is more rounded, the striae—which are finer and more numerous—never extend to the posterior ridge (Figure 20) let alone cross over it onto the posteroventral area of the valve's central section, and the upper limb of its pallial sinus is straighter—hence the entire sinus is broader anteriorly; the ground color of *G. convexa* is never marbled, and its rays (which are relatively broader) are generally less distinct from the background, its umbones are flushed with pale cream-yellow, pink or lavender, its internal glaze is thicker and more uniform, and finally there is neither the white umbonal area nor the brownish orange blotches of *G. radiata*.

Gari livida (Figures 14, 15, 21) from temperate southern Australia is smaller (to 45 mm), shorter, and heavier, its posterior margin is relatively broader, its left valve is flatter (but the commissure is straight), its surface bears numerous, fine, close, concentric cords, the striae on the posterior slope of the right valve are finer and more numerous (they do, however, reach the posterior ridge and/or cross it to become irregular lamellae like *G. radiata*) (Figure 21), the upper limb of the pallial sinus is straighter—hence the entire sinus is broader anteriorly; the ground color of *G. livida* is never marbled, its coloration—both externally and internally—is like that of *G. convexa*, and its rays are never visible at the ventral margin.

REEVE (1856) confused *Gari radiata* with *G. amethysta* (Wood) (Figures 18, 22), but *G. amethysta* is less closely related than either *G. convexa* or *G. livida*. *Gari amethysta* has a broader posterior end, more numerous concentric striae that always cover all the central area as well as the posterior slope on both valves, and its ground coloration is marbled violet-brown with distinct, darker rays.

Although it seems unlikely to me any modern author would follow LAMARCK (1818) and confuse *Gari radiata* with the eastern Atlantic-Mediterranean *G. (Gobraeus) virgata* (Lamarck), a brief comparison is justified. *Gari virgata* (Figure 16) is thicker, broader, more truncate posteriorly, and differently sculptured, and its pallial sinus is relatively broader. Both species have a purplish internal

glaze and brownish violet streak in the escutcheonal area of the posterodorsal margin.

Geographical Distribution

Within the tropical Indo-west Pacific, *Gari radiata* has a large, roughly triangular area of distribution. Its northern limit is Boso Peninsula, Honshû Island, Japan (KURODA *et al.*, 1971). Southwards, it extends through the South China Sea (SCARLATO, 1965) and Philippine Sea (REEVE, 1857; HIDALGO, 1903) to Indonesia (PRASHAD, 1932). Westwards, it extends through the Gulf of Thailand (LYNGE, 1909) and Bay of Bengal. The western extremity is the west coast of the island of Sri Lanka (REEVE, 1856). Thorough searches of collections made recently in the Marianas Islands, Papua New Guinea, New Caledonia, the Kermadec Islands, and northern Australia failed to reveal any specimens of *G. radiata*.

Habitat

According to KURODA *et al.* (1971), *Gari radiata* inhabits (presumably clean) sandy substrata from the intertidal zone to 10 m. I have not collected this species myself, so I cannot add any further information on habitat or ecology.

Material Examined

JAPAN: 6c (AMS C125620; NHMW 347; MNHN); 1c, Wakayama-ken, Honshû I. (AMS C74209); 1c, ELWN, Mikawa, Honshû Island (AMS C87763). HONG KONG: 5c, 1h (AMS 38771; BMNH 1936.1.8.224–225; CAS; MNHN). PHILIPPINE ISLANDS: 5c (BMNH; MNCN); 1c, Manila, Luzon Island (CAS). INDONESIA: 2c, Makassar (ZMB 25069—lectotype and paralectotype of *Psammobia denikei* Martens); 1h, Corindon, Makassar—01°56'S, 119°17'E (MNHN); 1c, Ambon Island (ZMB 25463—lectotype of *Psammobia radiata* Dunker in Philippi); 1c, Java (ZMB—paralectotype of *Psammobia radiata* Dunker in Philippi); 1c, Java (ZMUC); 1c, 10 m, near Onrust (ZMUC); 1c, Baai van Pidjot, Lombok Island (ZMA); 1c, Toedal, Kei Eilandeu (ZMA). MALAYSIA: 1h, on beach, Tanjong Rhu, N Pulau Langkawi, NW Malaysia—06°27'N, 99°50'E (AMS) 1c, Penang (MNHN). SINGAPORE: 1h, shallow water (ZMUC). THAILAND: 1c, 1h, 9–16 m, off Cape Liant and Mesam Island, Mellem (ZMUC); 1h, 3 m, Koh Kahdat (ZMUC). SRI LANKA: 10c (BMNH 1964018, 1964019; NHMW G9387; MNCN; MNHN); 4c, Gulf of Mannar (BMNH 1953.1.7.163–165). "INDIAN OCEAN": 2c (MNHN—specimens labelled "*Psammobia virgata* var. c" by Lamarck). UNKNOWN LOCALITY: 4c (MNHN; NHMW 347; G9387).

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Embryonic Stages of *Loligo bleekeri* Keferstein (Mollusca: Cephalopoda)

by

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Abstract. For observation of the embryonic development of *Loligo bleekeri*, a total of 12 fresh egg capsules were kept in a small aquarium at a temperature of $11.7 \pm 0.4^{\circ}\text{C}$, a salinity of ca. 34.00‰, and a photoperiodicity of 12L:12D in the laboratory. The period from spawning to hatching ranged from 64 to 67 days. The diameter of eggs ranged from 2.6 to 2.7 mm and mantle length of hatchlings from 3.0 to 3.3 mm. Twenty-eight embryonic stages defined by morphological features are described for *Loligo bleekeri*. The major developmental pattern of the species was mostly identical to that of *L. pealeii* and *L. forbesi*.

INTRODUCTION

A total of about 35 species of squids in the genus *Loligo* are known to occur in coastal and neritic waters of the world oceans (NESIS, 1987). *Loligo bleekeri* is distributed around Japan, South Korea, and the northern part of China (NESIS, 1987).

Neritic squids of the family Loliginidae are increasingly used as experimental material for neurophysiological research (ROSENBERG, 1973; ARNOLD *et al.*, 1974; MATSUMOTO, 1976), and they are also an important fishery resource (VOSS, 1973; OKUTANI, 1977; RATHJEN *et al.*, 1979).

Previous studies on the embryonic development of *Loligo bleekeri* (NISHIGAWA, 1868; ISAHAYA, 1934; ISAHAYA & TAKAHASHI, 1934; HAMABE, 1960) have described morphological changes with time. For comparative studies of different species, normal developmental stages of squid embryos are required.

This study, based on the above short notes, was done primarily to establish a standardized embryonic development scheme for *Loligo bleekeri* under stable environmental conditions.

MATERIALS AND METHODS

Fresh egg capsules from several captive adult females of *Loligo bleekeri* were collected 8 January 1991 and 13 April 1991, and transported to the laboratory. Twelve egg capsules were used in this study.

In the laboratory, four egg capsules were suspended in each of three beakers, each containing about 800 mL of

seawater, in an aquarium supplied with a running water system. Seawater in the beakers was renewed daily and aerated to prevent abnormal development.

The egg capsules were kept at a temperature of $11.7 \pm 0.4^{\circ}\text{C}$, the salinity was ca. 34‰, and the photoperiod was 12L:12D. The light intensity was maintained at 1900 lux during the light period (08:00–20:00) and 5 lux during darkness (20:00–08:00).

Observations were made four times each day from Stage 1 to Stage 9, and once a day from Stage 10 to Stage 28. In each observation, a few eggs were extracted randomly from the egg capsules. For detailed examination, the whitish outer coat and chorions were removed. The distribution of the chromatophores of the embryo at Stage 28 was drawn based on color transparencies of hatchlings.

The morphological staging criteria follow those of ARNOLD (1965) and SEGAWA *et al.* (1988). The 30-stage system of ARNOLD (1965) is widely used in cephalopods. Minor variation of stage numbers should be considered when classifying developmental stages, because there are heterochronies of the first appearance of some organ systems used as staging criteria with different species and there are also different authors' interpretations for the subdivisions. A 28-stage system was appropriate for *Loligo bleekeri*, and is used in this study.

RESULTS AND DISCUSSION

Egg development of *Loligo bleekeri*

Egg capsules measured 8–10 cm in length and contained about 40–50 eggs. Individual eggs were enveloped in sev-

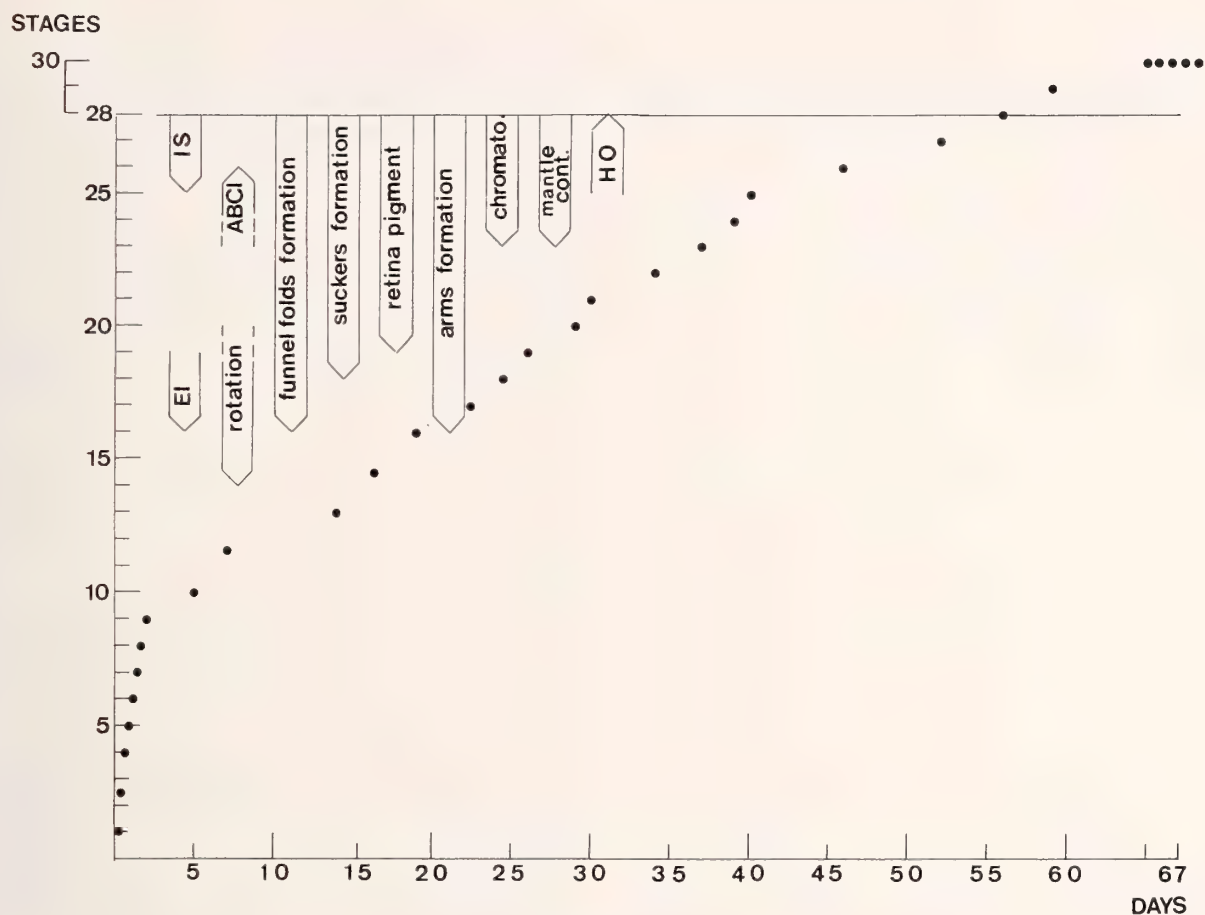


Figure 1

The sequence of appearance of major features in the embryonic development of *Loligo bleekeri*, and stage-time plot of *Loligo bleekeri* based on the stages defined by ARNOLD (1965) for *Loligo pealeii*. Key: ABC1, arm bases closure; chromato., chromatophore; EI, eye vesicle invagination; HO, Hoyle's organ; IS, ink sac; mantle cont., mantle contraction.

eral layers of spirally arranged jelly and covered with a thick, translucent, whitish flexible outer coat.

Development time was 9.5 weeks at $11.7 \pm 0.4^\circ\text{C}$. The incubating temperature adopted in this study was reported by HAMABE (1960) to be the most favorable for embryonic development. Almost all embryos in the egg capsules hatched during the night.

The embryonic development of *Loligo bleekeri* was classified into 28 stages as shown in Figure 3. Stages advocated by ARNOLD (1965) are indicated below in parentheses.

Stage 1 (A-1): Fertilization. Ooplasmic streaming forms blastodisc. Perivitelline space around animal pole appears to broaden. Eggs ellipsoidal in shape (length 2.6–2.7 mm, width 1.7–1.8 mm).

Stage 2 (A-2/3, 8 hr): Maturation division begins. Polar bodies appear.

Stage 3 (A-4, 15 hr): First cleavage. First furrow arising

in center of blastodisc. Blastodisc quite apparent but not elevated. Two-cell stage.

Stage 4 (A-5, 22 hr): Second cleavage. Second furrow crosses first at right angle. Blastodisc slightly elevated. Four-cell stage.

Stage 5 (A-6, 29 hr): Third cleavage. Division unequal. Eight-cell stage.

Stage 6 (A-7, 36 hr): Fourth cleavage. 16-cell stage.

Stage 7 (A-8, 43 hr): Fifth cleavage. 32-cell stage.

Stage 8 (A-9, 50 hr): Sixth cleavage. 64-cell stage.

Stage 9 (A-10, 5 days): Formation of ring-shaped germ cell layer. Yolk papilla evident. Formation of three germinal cell layers.

Stage 10 (A-11/12, 7 days): Yolk papilla flattened. Blastoderm spreading by marginal cell divisions.

Table 1

Summary of egg size, development time, and hatchling size in loliginid species of the genera *Loligo* and *Sepioteuthis*.

Taxa	Egg size (mm)	Development time (days)	Hatchling size (mm ML)	Temperature (°C)
<i>L. pealeii</i>	1.0–1.6 ¹	10–27 ²	1.6 ³	12–23 ²
<i>L. opalescens</i>	2.0–2.5 ⁴	30–35 ⁵	2.5–3.2 ⁶	13.6 ⁵
<i>L. vulgaris</i>	2.3–2.7 ⁷	45–70 ⁸	2.7 ³	12–14 ⁸
<i>L. bleekeri</i>	2.6–2.7	64–67	3.0–3.3	11.7 ± 0.4
<i>L. forbesi</i> ⁹	3.0–3.3	68–75	4.3–4.9	12.5 ± 0.5
<i>S. lessoniana</i> ¹⁰	5.6–5.8	23–26	5.0–7.0	25.0 ± 0.1

¹ SUMMERS (1983); ² McMAHON & SUMMERS (1971); ³ BOLETZKY & HANLON (1983); ⁴ FIELDS (1965); ⁵ MCGOWAN (1954); ⁶ MCCONATHY *et al.* (1980); ⁷ WORMS (1983); ⁸ MANGOLD-WIRZ (1963); BOLETZKY (1974); ⁹ SEGAWA *et al.* (1988); ¹⁰ SEGAWA (1987).

Stage 11 (A-13, 14 days): Blastoderm covers about one-third of egg surface.

Stage 12 (A-14/15, 16 days): Blastoderm covers about one-half of egg surface.

Stage 13 (A-16, 19 days): Blastoderm covers about two-thirds of egg surface.

Stage 14 (A-17, 22 days): Blastoderm nearly covers egg surface. Optic vesicle primordia appear as two thickened placodes on either side of embryo. Shell gland primordium visible at former animal pole. Embryo begins to rotate (very slow gliding movement generated by cilia on the yolk envelope; BOLETZKY, 1971; JOLL, 1978). Slight equatorial constriction appears, which future separates external yolk sac from developing embryo.

Stage 15 (A-18, 23 days): Outer yolk sac completely enveloped by blastoderm. Shell gland begins to invaginate and its border elevates. Peripheral elevation of eye rudiment distinct. Mantle primordium first visible.

Stage 16 (A-18+, 24 days): Ring folds enclose eye primordia and grow over central part of rudiments. Mouth appears as crescent-shaped invagination on oral surface of dorsal surface. Arm primordia appear as two thickened but not discrete bands of cells lateral to and in front of anterior funnel folds. Anterior and posterior funnel folds present as placodes on ventral surface.

Stage 17 (A-19, 26 days): Statocyst primordia appear as slight depression between anterior funnel fold and posterior funnel fold. Gill primordia appear as thickened placodes along with posterior funnel folds. Unpaired median anal papilla primordium visible between gill primordia. Arm primordia discrete and tentacles elongate. Mantle

grows toward both animal and vegetable poles. Mouth invagination distinctly visible.

Stage 18 (A-20, 29 days): Anterior and posterior funnel folds elevated and grow toward midline. Eye vesicles nearly closed. Sucker primordia first appear on tentacles. Distinct salivary pit in mouth. Gills apparent.

Stage 19 (A-21, 30 days): Shell gland completely closed. Transverse fin primordia appear on mantle but not yet distinct from surrounding mantle tissue. Anterior and posterior funnel folds fuse together. Granular particles appear in perivitelline space. First cup-shaped suckers on tentacles visible. Eye lens primordia faintly visible. Light red pigmentation of retina visible.

Stage 20 (A-22, 34 days): Distal edges of anterior funnel folds raise and bend toward midline. Mantle covers one-third of gills. Fins apparent. Suckers on arms III first appear. Eye lenses evident.

Stage 21 (A-23, 37 days): Retina cup-shaped. Mantle covers one-half of gills. Funnel folds fuse anteriorly.

Stage 22 (A-24, 39 days): Two-thirds of gills covered by anterior-growing mantle. Median margins of funnel folds fuse; funnel retraction muscles still visible. Statocysts fully developed with statoliths. Branchial hearts formed at bases of gills and start to beat irregularly. Suckers on arms IV appear. Iris curved but not pigmented. Gill leaflets visible.

Stage 23 (A-25, 40 days): Iris begins to be pigmented. Retina turns dark red-brown. Posterior portion of funnel covered by mantle. Gill leaflets visible through mantle wall. Systemic heart starts to beat. Red chromatophores visible on ventral mantle surface. Mantle contractions observed. Posterior lobes of internal yolk sac increase in size. External yolk sac still longer than embryonic body.

Stage 24 (A-26, 46 days): Tentacle and lateral arm bases extend as folds that cover about one-half of optic ganglion on each side (*cf.* NAEF, 1928). Red chromatophores present on tentacles, arms IV, ventral and dorsal head, and surface of dorsal mantle.

Stage 25 (A-27, 52 days): Hoyle's organ evident on posterior dorsal mantle between fins. Ventral arm bases cover one-half to two-thirds of eye vesicles. Ink sac begins producing ink. First red chromatophores observed on arms II. External yolk sac approximately same length as mantle.

Stage 26 (A-28, 56 days): Ink sac filled with ink. Second and third row of chromatophores appear on tentacles. Second row chromatophores yellow; third row chromatophores small, red. Mid-gut gland and caecum prominent. External yolk sac approximately equal to head length. Olfactory tubercles clearly visible on each side of ventral surface of head.

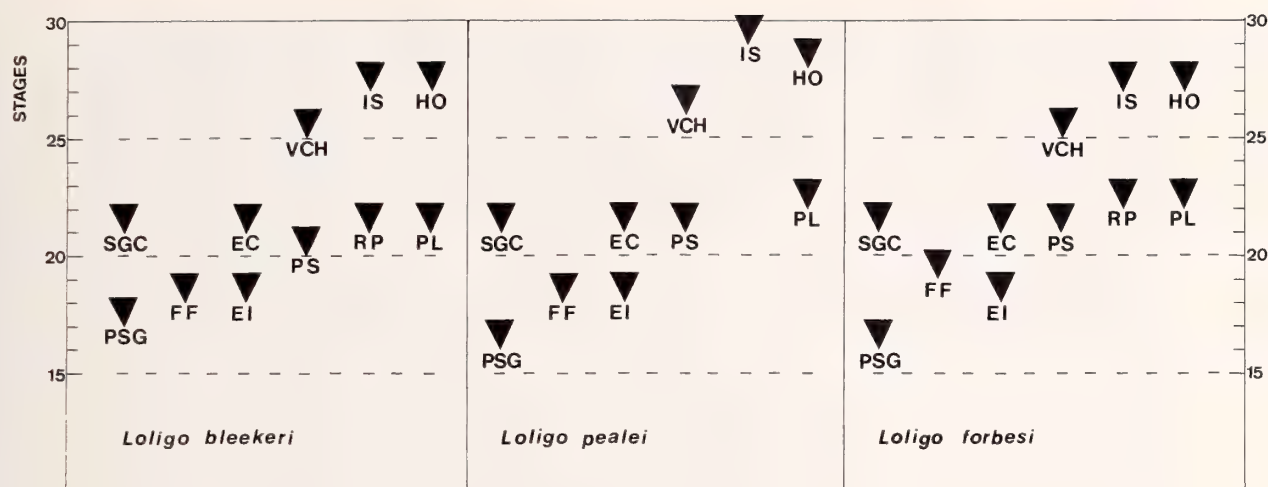


Figure 2

Comparison of chronological appearance of select organs in three species of the genus *Loligo*, using ARNOLD's (1965) stage system. Key: EC, eye vesicle closed; EI, eye vesicle invagination begins; FF, funnel formation begins; HO, Hoyle's organ appears; IS, ink sac appears; PL, primordium of lens visible; PS, primordia of suckers appear; PSG, primordium of shell gland appears; RP, retina pigmentation begins; SGC, shell gland closed; VCH, ventral mantle chromatophores appear.

Stage 27 (A-29, 59 days): Chromatophores first appear on arms III. External yolk sac approximately equal to length of tentacles.

Stage 28 (A-30, 64–67 days): Hatching. Small external yolk sac dropped and Hoyle's organ becomes depleted. Internal yolk sac remains as small triangular body. Shortly after hatching, larvae swim toward water surface with mantle pointing upward. Hatchling mantle lengths are 3.0–3.3 mm. Chromatophore patterns relatively regular on ventral and dorsal head and on dorsal mantle, but, among individuals, highly asynchronous on ventral mantle.

Comparison of Embryonic Development Among Three *Loligo* Species

Based on the observed sequence of development of the major embryonic features, the developmental pattern of *Loligo bleekeri* was compared to that of *L. pealeii* (ARNOLD, 1965). The results are shown in Figure 1. In this figure, for the sake of convenient comparison, developmental stages of *L. bleekeri* were aligned to those of ARNOLD (1965) with the criteria shown in the former section. Within the first five-day period, the eggs of *L. bleekeri* developed rapidly from Stage 1 to Stage 10. Thereafter, the developmental pattern of the eggs became linear with a gentle slope. This developmental pattern in *L. bleekeri* was almost the same as that observed in *L. pealeii* by ARNOLD (1965). In contrast, SEGAWA *et al.* (1988) found a sigmoid curve in the internal organogenesis of *L. forbesi*.

Appearance of Some Organ Rudiments in Squid Embryos

The developmental length and size of hatchlings depend largely on the size of the spawned egg (MANGOLD *et al.*, 1971; SEGAWA *et al.*, 1988). Although about 35 *Loligo* species are distributed in shallow neritic waters around the world (NESIS, 1987), embryonic development is poorly known except for a few species.

Information on egg size, development time, and hatchling size of six species of the family Loliginidae are summarized in Table 1. In comparison to other species, *L. bleekeri* has relatively larger eggs (2.6–2.7 mm) and a longer development time (64–67 days).

As seen in Table 1, the development time and mantle length of hatchlings increase as egg size increases. If these differences are valid, then species-specific differences in the first appearance of some organs, relative to stages, may exist. At present three loliginid species—*Loligo bleekeri*, *L. pealeii*, and *L. forbesi*—are available for comparison (see Figure 2).

The pattern of chronological appearance of organs is quite similar between the species of *Loligo* so far examined. However, several differences in the chronology of appearance are evident between two or three species (Figure 2): for example, the primordium of the shell gland, PSG; funnel formation, FF; primordia of suckers, PS; retina pigmentation, RP; primordium of lens, PL; ventral mantle chromatophores, VCH; ink sac, IS; Hoyle's organ, HO. In all instances, differences among species were restricted

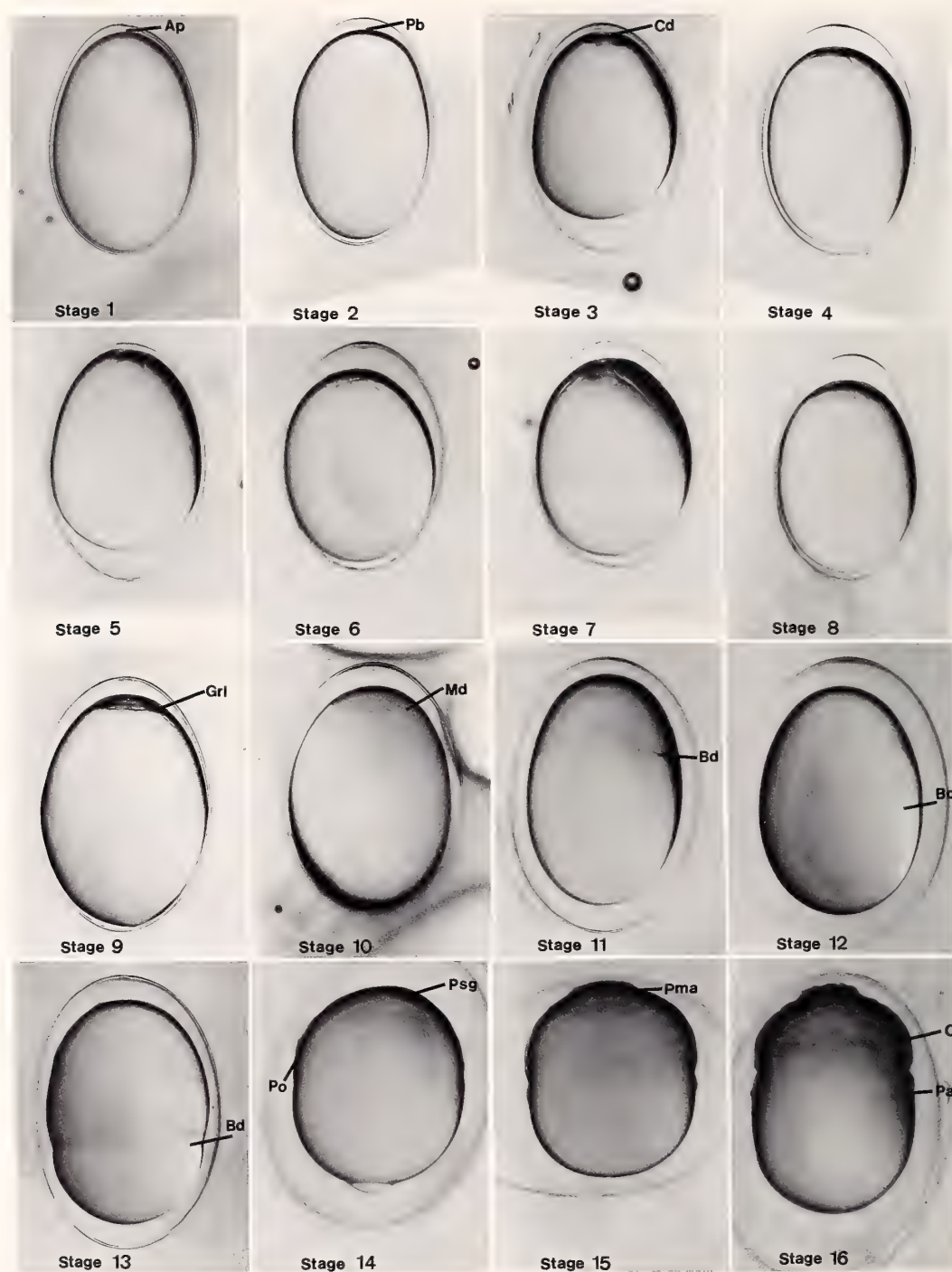


Figure 3 (Part 1)



Figure 3 (Part 2)

Figure 3

Stages 1–28 in the embryonic development of *Loligo bleekeri*. Dorsal (D), ventral (V) or laterodorsal (LD) views. Key: A, anal papilla; Ab, arm bases; Aff, anterior funnel fold; Ap, animal pole; Bd, blastoderm; Cd, cell division; Ce, caecum; Ch, chromatophore; F, fin; G, gill; Gl, gill leaflets; Grl, germ-ring layer; Ho, Hoyle's organ; Ir, iris; Is, ink sac; Iy, internal yolk sac; L, lens; M, mouth; Ma, mantle; Md, marginal division; Mg, mid-gut gland; O, optic vesicle; Of, olfactory tubercle; Pa, primordia of arms; Pb, polar body; Pf, primordium of fin; Pff, posterior funnel fold; Pl, primordium of lens; Pma, primordium of mantle; Po, primordium of optic vesicle; Psg, primordium of shell gland; Pst, primordium of statocyst; Py, posterior lobes of inner yolk; Rp, retina pigmentation; Stl, statolith; Su, sucker; T, tentacle; A2, arm II; A3, arm III; A4, arm IV; HD, dorsal side of head; HV, ventral side of head; MD, dorsal side of mantle; MV, ventral side of mantle; r, red chromatophore; y, yellow chromatophore.

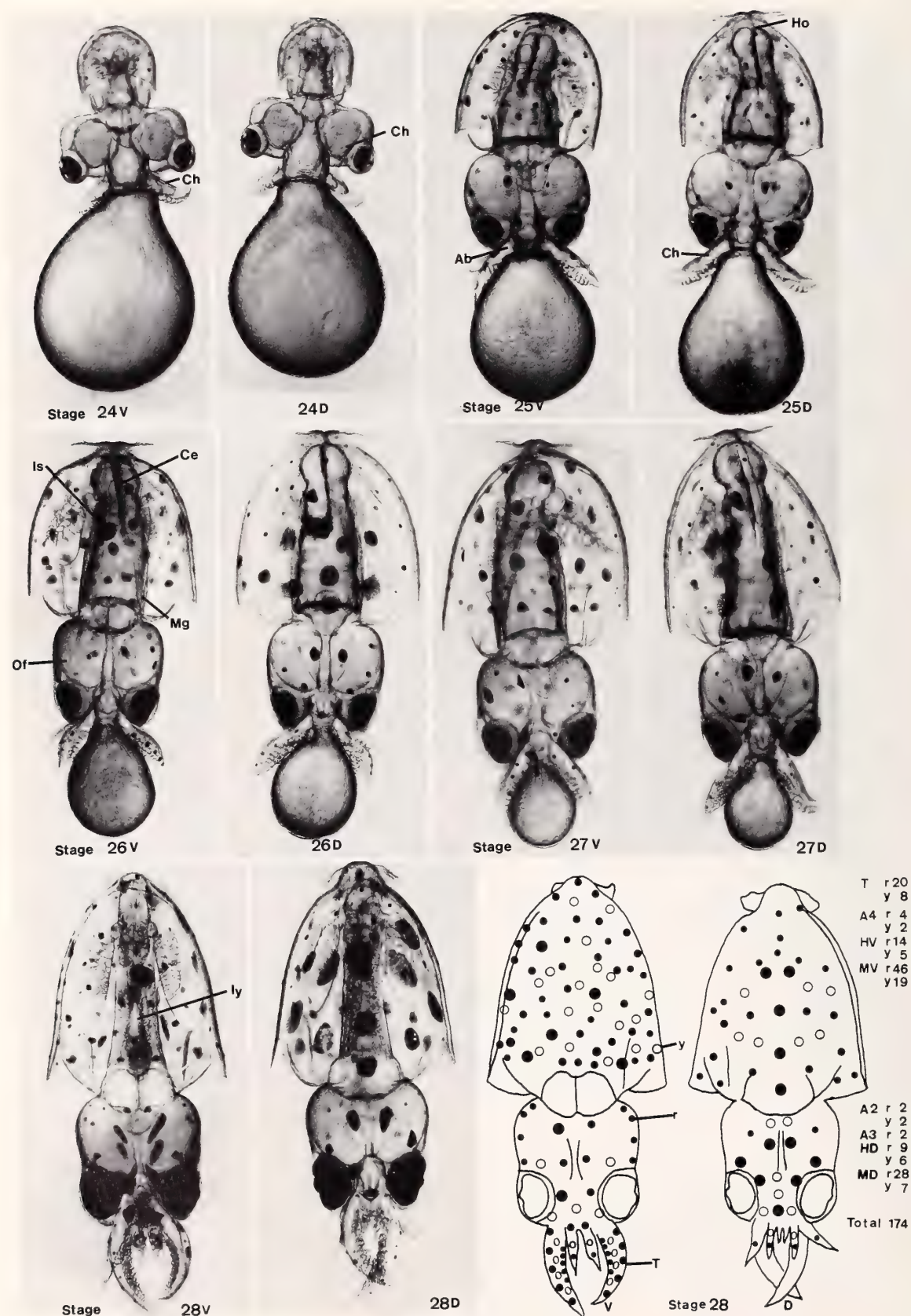


Figure 3 (Part 3)

within a narrow range of not more than three stages. This extreme homogeneity in the morphological development of loliginid squids has been previously reported by HUNTER & SIMON (1975).

Recently, NATSUKARI (1984) placed *Loligo bleekeri* and *L. pealeii* in a separate genus, *Heterololigo*, because of several distinct morphological characteristics, including the presence of a well-developed medial and longitudinal crest on the mid-portion of the modified part of the hectocotylized arm.

A distinct similarity in the developmental patterns of the two *Heterololigo* species compared to those of *Loligo bleekeri* and *L. forbesi* was not found. In *Loligo* species, the degree of similarity in developmental processes seems to depend solely on egg size.

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NOTES, INFORMATION & NEWS

Erratum, Volume 34, Number 3 A. Solem, Australian Land Snails

Incorrectly merged computer files resulted in an error in the originally submitted manuscript by Alan Solem ("Distribution and diversity patterns of Australian pupilloid land snails"), published posthumously in the July 1991 issue—34(3):233–252.

The error was noticed by Vince Kessner, Darwin, Australia, for whose diligence we are grateful.

According to Margaret Baker, Field Museum of Natural History, Chicago, Illinois, the following entries are correct and should replace the incorrect entry on page 249 (*Gyliotrachela napierana*).

Gyliotrachela napierana Solem, 1981

See SOLEM, 1981:90–91, figs. 1, 2, 9, 13; SOLEM, 1989:502–503, figs. 91–93.

Type locality: 5.9 km NW of Yammera Gap, Napier Ranges, Western Australia.

Gyliotrachela ningbingia Solem, 1981

See SOLEM, 1981:91, figs. 3, 4, 10, 14–16, 18, 19; SOLEM, 1989:503–504, figs. 94–96.

Type locality: 5.7 km N of No. 8 Bore, Ningbing Ranges, N of Kununurra, Western Australia.

International Commission on Zoological Nomenclature: Applications and Opinions

The following applications and opinions were published on 26 March 1992 in Volume 49, Part 1 of the *Bulletin of Zoological Nomenclature*. Comment or advice on the applications is invited for publication in the *Bulletin*, and should be sent to the Executive Secretary, ICZN, % The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Case 2247—*Balea* Gray, 1824 (Mollusca: Gastropoda): proposed conservation of name, currently in use for a genus of pulmonate gastropods, which is threatened by the senior objective synonym *Strombiformis* Da Costa, 1778.

Case 2634—*Xeromunda* Monterosato, 1892 (Mollusca: Gastropoda): proposed designation of *Helix candiota* Mousson, 1854, as the type species.

Opinion 1662—*Limax fibratus* Martyn, 1784, and *Nerita hebraea* Martyn, 1786 (currently *Placostylus fibratus* and *Natica hebraea*; Mollusca, Gastropoda): specific names conserved, and *Placostylus* Beck, 1837: *L. fibratus* designated as the type species.

Opinion 1663—*Fryeria* Gray, 1853, and *F. rueppelii* Bergh, 1869 (Mollusca: Gastropoda): conserved.

Opinion 1664—*RISSOIDAE* Gray, 1847 (Mollusca: Gastropoda): given precedence over *TRUNCATELLIDAE* Gray, 1840.

Opinion 1665—*Potamilus* Rafinesque, 1818 (Mollusca: Bivalvia): not suppressed.

American Society of Zoologists 1992 Meeting

The American Society of Zoologists, with the American Microscopical Society, Animal Behavior Society, The Canadian Society of Zoologists, The Crustacean Society, and The International Association of Astacology, will hold its annual meeting in December, in Vancouver, B.C., Canada.

The deadline for abstracts is 31 July 1992.

Several interesting symposia and workshops are scheduled.

For more information, contact: Mary Adams-Wiley, Executive Officer, ASZ, 104 Sirius Circle, Thousand Oaks, CA 91360. Phone: (805) 492-3585.

BOOKS, PERIODICALS & PAMPHLETS

The Malacofauna of Hong Kong and Southern China, Volumes I and II

The Malacofauna of Hong Kong and Southern China, edited by BRIAN MORTON. 1980 [reprinted 1986]. vi + 345 pp. Price: \$40. *The Malacofauna of Hong Kong and Southern China*, II, edited by BRIAN MORTON & DAVID DUDGEON. 1985. Volume 1: vii + 362 pp.; Volume 2: viii + 363–681 pp. Price: \$80. Hong Kong University Press, 139 Pokfulam Road, Hong Kong.

These important volumes contain more useful information about marine mollusks than most journals do in two or three years. Some non-marine mollusks are also treated. The books are the products of the periodic workshops on mollusks pioneered by Brian Morton. The session that led to the first volume was held in 1977, the second in 1983. They contain papers that will be of interest and utility for nearly every malacologist.

The first volume is divided into sections on taxonomy, ecology, and functional morphology. Highlights of the taxonomic section include studies on the bivalve families Veneridae and Corbiculidae, gastropod limpets and the Neritidae, and chitons. The ecology section includes papers on the diets of predatory gastropods and on the correlation of gill function to intertidal distribution of bivalves. The functional morphology section has papers on the bivalves *Caecella*, *Veremolpa*, *Coralliophaga*, *Vulsella*, and *Arcuatula*, and the gastropod *Crepidula*.

The second workshop resulted in two volumes, divided into sections on taxonomy, morphology, ecology, physiology, and behavior. The taxonomy section has particularly important papers on the Donacidae, Mytilidae, Potamididae, Caecidae, and Vermetidae. The morphology section has key papers on the Caecidae, Arcidae, Isognomonidae, Veneridae, and bivalve stomachs. The ecology section features papers on *Pinna*, Littorinidae, *Perna*, and several freshwater gastropods, including *Biomphalaria*. The phys-

iology section has papers on several bivalves and on the thermal tolerances of mangrove gastropods. The behavior section includes prey selection by *Octopus*, naticid predation, nudibranch feeding, and freshwater gastropod foraging strategies.

A third workshop has recently been held and, no doubt, interesting reports will appear in print in two or three years.

Gene Coan

Two Volumes Noted

Manglares y Hombres del Pacifico Colombiano, by HENRY VON PRAHL, JAIME R. CANTERA & RAFAEL CONTRERAS. Colombia (Fondo para la Protección del Medio Ambiente "José Celestino Mutis"). 193 pp., illustrated. April 1990.

Covers the distribution and biology of mangrove ecosystems along the Pacific coast of Colombia. Pages 113–116 list mollusks.

Dvustvorchatye molliuski shel'fov i kontinental'nogo sklona severnoi Patsifiki [Bivalve Mollusks of the Shelf and Continental Slope of the North Pacific Ocean], by ALEXANDER I. KAFANOV. Post-4 July 1991. Akad. Nauk. SSSR, Dal'nevostochnoe Otdelenie, Institut Biologii Moria. 198 pp.

A checklist covering the North Pacific, south to Japan and central California. Localities are indicated by a numerical code keyed to maps, and depths are given. The bibliography is brief and the index is thorough.

Gene Coan

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, *not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete, with all journal titles *unabbreviated*, and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *The Veliger* 4:132-134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

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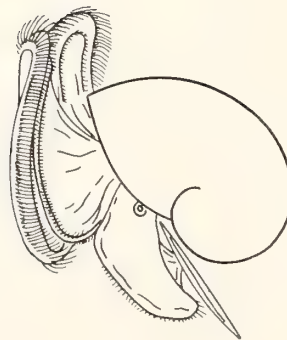
Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.

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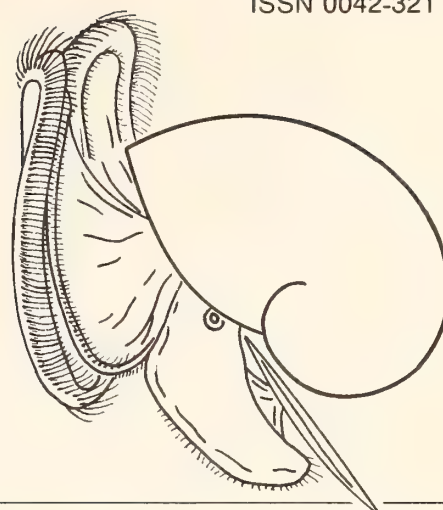
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This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, evolutionary, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Reproduction and Development of Trochacean Gastropods

by

CAROLE S. HICKMAN

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University of California, Berkeley, California 94720, USA

Abstract. A compilation of comparative data on reproduction and development of trochacean gastropods (Prosobranchia: Archaeogastropoda) is presented and analyzed within the framework of the revised suprageneric classification of the superfamily. The traditional portrayal of the male and female reproductive anatomy and gametes as simple and unspecialized is contrasted with the diversity and complexity of elaborations of the epipodium that may function in sperm transfer, elaborations of glandular mantle tissue (urogenital papillae) that produce a variety of primary and secondary gelatinous egg coverings that affect buoyancy and clumping properties of gametes, and evidence of unexpected modifications of trochacean sperm. Considerable variation occurs in the periodicity and control of both gametogenesis and spawning, but there is no common or dominant pattern characterizing either higher taxa or ecological settings. In addition to the two common modes, broadcast spawning with pelagic development and spawning of benthic egg masses with benthic development, brooding has arisen independently in at least one turbinid subfamily and three trochid subfamilies. A fourth mode, mixed development, occurs in several taxa that extrude eggs, either as strings that sink to the bottom or that are loosely tacked to the bottom for a benthic phase preceding the pelagic phase. The positions of hatching and settlement within the developmental sequence are highlighted as evolutionarily significant variables in a table and comparative diagram of trochacean developmental stages and events. Hatching of pelagic larvae may occur as early as the trochophore and as late as the post-torsional veliger stage, and settlement may precede the completion of torsion.

Popular classifications of molluscan developmental modes and "strategies" are not useful because they underestimate the range of variation in trochacean development. The possibility of feeding by planktic trochacean larvae, as well as the possibility of feeding by benthic larvae between settlement and metamorphosis, merits renewed attention. Problems of interpretation of the trochacean protoconch include documentation of the nature and extent of heterostrophy and investigation of a poorly understood process of asymmetric mechanical deformation of the organic larval shell that precedes mineralization.

INTRODUCTION

As one of the most primitive groups of living marine gastropods, trochaceans have been characterized as having uniformly simple reproductive systems and simple reproductive and developmental patterns featuring broadcast spawning, external pelagic fertilization, and a brief, non-feeding (lecithotrophic) planktic larval stage. Although the conventional generalities provide a convenient backdrop for portraying the evolution of caenogastropod reproductive diversity, they mask the wellspring of diversity and

flexibility that have served this geologically ancient group throughout 500 million years of evolutionary experimentation. Data on reproductive biology and early development of living trochaceans are scattered in the literature. Because of a recent increase in the number of more detailed studies of individual species, the time is ripe to produce a synthesis and interpretation.

Until recently, few reproductive or developmental studies have been experimental or carried out under controlled conditions, and UNDERWOOD (1972b) attributed this to the difficulty of inducing spawning and of rearing of larvae under laboratory conditions. Improved techniques for maintaining reproductively mature adults, inducing spawning, and culturing embryos and larvae (see STRATH-

¹ This is contribution Number 1560 of the Museum of Paleontology.

MANN, 1987) provide new opportunities to move beyond anecdotal accounts of individual events to characterization of the range of reproductive patterns that have evolved within the superfamily.

Most observations to date are of temperate intertidal species, and the taxa that have been studied most intensively are trochids in the subfamilies Margaritinae, Trochinae (tribes Gibbulini and Cantharidini), and Calliostomatinae. Little is known about reproduction and development in the turbinid subfamilies, and there are no data for members of the Skeneidae.

Studies of individual trochacean species have never been set in a comparative systematic framework, nor has there been an adequate trochacean classification to serve as a basis for comparative study. It is therefore appropriate to evaluate both the strengths and the gaps in our knowledge of trochacean reproduction and development in the context of the new classification and systematic revision of the superfamily (HICKMAN & MCLEAN, 1990), summarized in Table 1. This paper is a supplement to that systematic revision and also a critique of some of the theory in molluscan reproduction and development.

Controversial issues examined in this paper include the possibility of evolution of a penis or penis-like structures in trochaceans, the possibility of ovoviviparity, the possibility of a special type of heterostrophy in trochacean shell growth, and the possibility of feeding in both pelagic and benthic trochacean larvae prior to metamorphosis.

Major objectives of this paper are: (1) to document variability in trochacean reproductive and developmental patterns within the systematic framework of the superfamily, (2) to identify gaps in comparative data and opportunities for future research, (3) to introduce an expanded set of spawning categories with examples of species in each category, (4) to present a table of stages in trochacean development that identifies major events within each stage and emphasizes the events that are variable in their timing, (5) to provide a summary set of illustrations of trochacean developmental stages, and (6) to illustrate the developmental patterns in trochaceans in a comparative manner that emphasizes their variability and versatility in contrast to those of caenogastropods, the group that heretofore has provided much of the vocabulary and theoretical framework for characterizing prosobranch reproduction and development.

MALE AND FEMALE REPRODUCTIVE ANATOMY

Gonads and Reproductive Tract

Trochaceans are all dioecious, but males and females are not usually distinguishable by shell features or external features of the animal. When removed from the shell, sexes are distinguishable without dissection, if the gonads are ripe, by the distinctly granular appearance of the ovary in

contrast to the smooth appearance of the testis. While color alone is not a reliable guide, female gonads are frequently green or greenish gray and male gonads are frequently creamy white or pink (Hickman, personal observation). The major features of the male and female reproductive systems are shown diagrammatically in Figure 1. PURCHON (1968) characterized this grade of reproductive organization as so simple as to approximate that of the hypothetical ancestral mollusk. Even though the trochacean genital tract lacks the degree of distal elaboration seen in the pallial oviduct (and associated glands) of more derived prosobranchs, the reproductive plumbing is more complicated than that of patellogastropods. It is made up of the same three basic components identified by FRETTER (1946) as common to all prosobranchs: gonadal, renal, and pallial. In both sexes the ripe gametes pass from the gonad (1) through a short gonoduct to the renopericardial duct (2) through the renopericardial duct to the right kidney, which in turn opens into the mantle cavity (3) through mantle tissue which may form a simple aperture (especially in males), an aperture surrounded by glandular lips, or (especially in females) a greatly enlarged glandular duct of mantle tissue protruding into the mantle cavity as a "urogenital papilla" (FRETTER, 1946, 1955; FRETTER & GRAHAM, 1962; HADFIELD & STRATHMANN, 1990).

Function of Female Urogenital Papillae and Pallial Glands

Glandular pallial tissue secretes mucus that constitutes at least part of the secondary jelly coatings in species that spawn eggs in strings or benthic egg masses (FRETTER & GRAHAM, 1962). However, HADFIELD & STRATHMANN (1990) were unable to find a correlation between the amount of jelly produced and the sizes of urogenital papillae, and the function of papillae merits additional study. The presence of a prominent papilla cannot be used as a criterion for inferring benthic development: a large papilla is present in females of species of *Calliostoma* that undergo predominantly pelagic development (HADFIELD & STRATHMANN, 1990:fig. 8), whereas there is little difference between the slightly enlarged lips surrounding the urogenital openings in males and females of cantharidine species that deposit strings of eggs on seagrass blades (Hickman, personal observation).

GERSCH (1936) suggested that secretions of the hypobranchial gland (mucus-secreting glandular pallial tissue) contribute to the formation of secondary jelly coatings, but there are no data to support or refute this hypothesis. The function of the prosobranch hypobranchial gland is speculative, and the histochemistry of its secretions is not well documented (FRETTER & GRAHAM, 1962). Gersch's inference was based on observation that hypobranchial secretion was more copious during the breeding season in *Gibbula tumida* (Montagu, 1803), a species that spawns benthic egg masses.

Table 1

Outline classification of trochacean gastropods identifying subfamilies and tribes for which there are published data on reproduction and development (solid circles) and subfamilies and tribes for which no data are available (open circles). Isolated observations or reports of single features do not qualify a taxon for a solid circle, and open circles identify taxa in which full comparative studies of reproduction and development are needed.

Superfamily TROCHACEA	Data	No data
Family TURBINIDAE Rafinesque, 1815		
Informal Group LIOTIINAE + ANGARIINAE		
Subfamily LIOTIINAE Adams & Adams, 1854		○
Subfamily ANGARIINAE Thiele, 1921		○
Informal Group MOELLERIINAE + COLLONIINAE		
Subfamily MOELLERIINAE Hickman & McLean, 1990		○
Subfamily COLLONIINAE Cossmann, 1916		○
Informal Group PRISOGASTERINAE + TURBININAE		
Subfamily PRISOGASTERINAE Hickman & McLean, 1990		○
Subfamily TURBININAE Rafinesque, 1815	●	
Informal Group GABRIELONINAE + TRICOLIINAE + PHASIANELLINAE		
Subfamily GABRIELONINAE Hickman & McLean, 1990		○
Subfamily TRICOLIINAE Woodring, 1928	●	
Subfamily PHASIANELLINAE Swainson, 1840		○
Family TROCHIDAE Rafinesque, 1851		
Informal Group TEGULINAE + EUCYCLINAE + MARGARITINAE		
Subfamily TEGULINAE Kuroda, Habe, & Oyama, 1971		○
Subfamily EUCYCLINAE Koken, 1897		
Tribe EUCYCLINI Koken, 1897		○
Tribe CHILODONTINI Wenz, 1938	●	
Tribe CALLIOTROPINI Hickman & McLean, 1990		○
Subfamily MARGARITINAE Stoliczka, 1868		
Tribe MARGARITINI Stoliczka, 1868	●	
Tribe GAZINI Hickman & McLean, 1990		○
Informal Group TROCHINAE + STOMATELLINAE + CALLIOSTOMATINAE + SOLARIELLINAE		
Subfamily TROCHINAE Rafinesque, 1815		
Tribe TROCHINI Rafinesque, 1815	●	
Tribe GIBBULINI Stoliczka, 1868	●	
Tribe CANTHARIDINI Cotton, 1959	●	
Subfamily STOMATELLINAE Gray, 1840		○
Subfamily CALLIOSTOMATINAE Thiele, 1924	●	
Subfamily SOLARIELLINAE Powell, 1951		○
Informal Group HALISTYLINAE + LIRULARIINAE + UMBONIINAE		
Subfamily HALISTYLINAE Keen, 1958		○
Subfamily LIRULARIINAE Hickman & McLean, 1990	●	
Subfamily UMBONIINAE Adams & Adams, 1854		
Tribe MONILIINI Hickman & McLean, 1990		○
Tribe BANKIVIINI Hickman & McLean, 1990		○
Tribe UMBONIINI Adams & Adams, 1854	●	
Subfamilies of uncertain affinity		
Subfamily CATAEGINAE McLean & Quinn, 1987		○
Subfamily TROCHACLIDINAE Thiele, 1928		○
Subfamily THYSANODONTINAE Marshall, 1988		○
Family SKENEIDAE Clark, 1851		○

Epipodial Elaborations and the Possibility of a Trochacean Penis

Isolated reports of a penis in trochaceans have been ignored or treated with skepticism. In the family Skeneidae, CLARK (1852), JEFFREYS (1865), and HÖISÆTER (1968) described a penis posterior to the right cephalic tentacle.

However, the structure is present in both males and females, and its function is unclear. FRETTER & GRAHAM (1977) referred to it instead as a "postoptic tentacle" and MARSHALL (1988b) as a "suboptic tentacle" that may be compound.

A more compelling account of a trochacean penis occurs in an overlooked paper by DALL (1889a), who claimed to

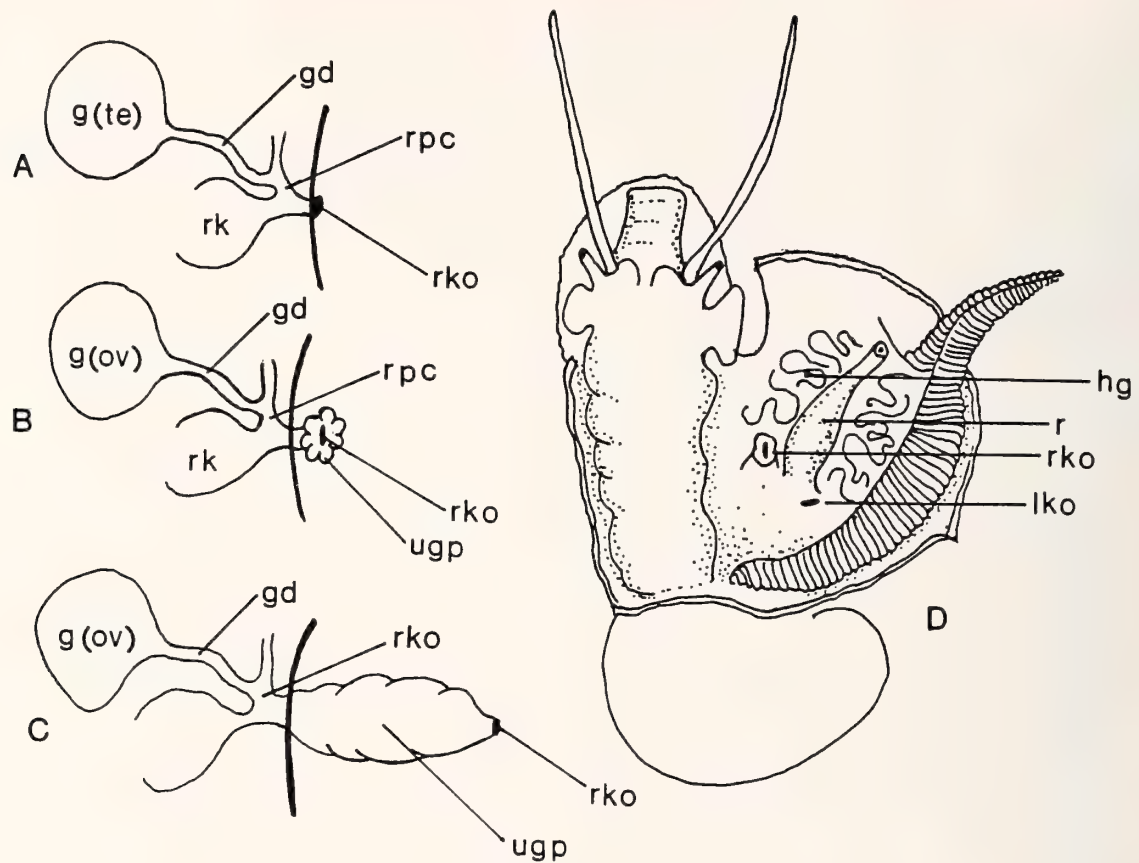


Figure 1

Male and female reproductive anatomies of trochacean gastropods. A. Schematic depiction of the male reproductive system (after FRETTER & GRAHAM, 1962). B. Schematic depiction of a female reproductive system with a small urogenital papilla (after FRETTER & GRAHAM, 1962). C. Schematic depiction of the female reproductive system with an enlarged urogenital papilla (after FRETTER & GRAHAM, 1962). D. Adult female of a *Prothalotia lehmanni* (Menke, 1843) (subfamily Trochinae, tribe Cantharidini) in mantle-cavity dissection with the mantle cut along the left side and laid back to the right to show the position of the urogenital papilla and urogenital opening (rko) relative to the rectum (r), hypobranchial glands (hg), and simple left kidney opening (lko). In both males and females, gametes pass from the single gonad (g), an ovary (ov) or testis (te), through two sections of duct, the first of gonadal derivation (gd) and the second of nephridial origin (renopericardial duct, rpc), and discharge into the mantle cavity via an opening that is simple in males but which may be further elaborated in females into a glandular duct or urogenital papilla (ugp).

have observed an "intromittent male organ" in "several" deep-sea trochaceans, proposing that it was a primitive structure that has been lost in shallow-water species. He gave a detailed description for the eucycline species *Caliotropis infundibulum* (Watson, 1879) of a small tubular structure lying above an elaborately modified right epipodial flap and stated: "The object of this apparatus is self-evident. The cylinder serves as a conduit for the seminal fluid ejected from the verge." This remarkable structure is almost certainly the same thing that WARÉN & BOUCHET (1989) have described in *Bathymargarites symplector* Warén & Bouchet, 1989. Although they state (p. 92) that it is the left neck lobe that has been modified, this is clearly a *lapsus*, because they illustrate it (figs. 105, 107) on the right side of the animal.

It is debatable whether the structure described by DALL (1889a) and WARÉN & BOUCHET (1989) should be called a penis or copulatory structure, insofar as it is not designed for insertion into the female and internal fertilization. However, any elaboration of the male exhalant right neck lobe that can direct the delivery of sperm is a step away from broadcast spawning in the direction of internal fertilization.

GAMETOGENESIS, GAMETES, AND REPRODUCTIVE PERIODICITY

UNDERWOOD (1972a) provided a detailed description of the stages in spermatogenesis and oogenesis from histological sections of the gonads of three British gibbuline

trochids that he sampled monthly. The most significant result of this program was rigorous documentation of a seasonal pattern of fluctuation in both the proportion of mature oocytes and the quantity of ripe sperm in two of the species [*Monodonta lineata* (da Costa, 1778) and *Gibbula umbilicalis* (da Costa, 1778)] in contrast to constant proportions in the third species (*G. cineraria* Linnaeus, 1758). Comparative histological data are lacking for representatives of other trochacean subfamilies and tribes and are required before patterns of gametogenesis can be examined in a systematic context.

Eggs and Primary Gelatinous Egg Coverings

The typical mature trochacean oocyte is a yolk-rich structure, of 150–300 μm diameter, enclosed by a clear membrane (the “envelope” of STRATHMANN [1987], “egg covering” of FRETTER & GRAHAM [1962], and “primary egg membrane,” “vitelline membrane,” or “fertilization membrane” of various other authors). The granular, yolk oocyte and the clear, enclosing membrane that is secreted by the oocyte are in turn covered by gelatinous coatings.

The complex gelatinous coatings of trochacean eggs may be a unique derived feature of the superfamily. There is no convincing documentation of analogous or homologous coatings in studies of more primitive prosobranch taxa, and they merit more careful study and characterization. Three different kinds of trochacean egg jellies are recognized herein: (1) an inner primary (ovarian origin) layer that surrounds mature oocytes, (2) an outer primary (ovarian origin) layer that swells upon contact with seawater and may disperse soon after spawning, and (3) secondary (pallial origin) jellies that bind individual oocytes together in strings, clumps, or masses.

The composition, properties, and function of the primary and secondary egg jellies are unresolved. Descriptions of gelatinous coatings of trochacean eggs have not used a uniform terminology (*cf.*, LEBOUR, 1937; FRETTER, 1955, 1984; FRETTER & GRAHAM, 1962; DESAI, 1966; UNDERWOOD, 1972a, b; HESLINGA, 1981; STRATHMANN, 1987; HOLYOAK, 1988a; HADFIELD & STRATHMANN, 1990), and the primary and secondary jellies have been treated as a single homogeneous unit in some accounts.

While there appear to be two distinct primary envelopes under light microscopy (Hickman, personal observation), FRETTER & GRAHAM (1962:322) suggested that they are fundamentally similar, with a line of contact between a denser inner jelly and a thinner superficial layer. Even if the two layers are not chemically distinct or separated by a membrane, they have physical properties that cause them to behave differently. DESAI (1966) observed (in *Monodonta lineata*) that on contact with seawater there was rapid swelling of the outer layer that made the eggs buoyant. He also noted that the outer coating dispersed within 20 minutes of spawning and that eggs sank. UNDERWOOD (1972b) observed (in *Gibbula cineraria*) not only that the outer coating dispersed soon after spawning, but also that

it was resistant to the penetration of sperm. This led him to propose an alternative function, that of initially blocking polyspermy. HADFIELD & STRATHMANN (1990) also noted dispersion of the jelly coat following spawning in *Margarites pupillus* (Gould, 1849) but did not speculate on its function.

Swelling of jelly coats after spawning has been noted in other taxa. HOLYOAK (1988a) reported expansion in two envelopes, which he described as an outer “gelatinous coat” and a “space” between the egg and the gelatinous coat, in *Calliostoma ligatum* (Gould, 1849). He did not indicate how long the swollen gelatinous envelope persisted. HESLINGA (1981) reported a single “pitted” jelly coat surrounding the eggs of *Trochus niloticus* (Linnaeus, 1758) that underwent post-fertilization swelling and persisted until hatching, leading him to propose that it functioned to reduce the sinking rate of embryos.

Primary gelatinous egg coverings are secreted in the ovaries, as originally suggested by FRETTER & GRAHAM (1962). Direct evidence of ovarian origin is provided by UNDERWOOD (1972a), who observed gradual deposition of the jelly coat late in oogenesis and used presence of the jelly coat to define mature oocytes. UNDERWOOD (1972b) further noted that mature oocytes dissected from the ovary for artificial fertilization showed the same swelling of the outer layer of the jelly coat on contact with seawater. Swelling of mature oocytes on contact with seawater is easily observed in fresh ovarian dissections and is common in trochacean species I have examined.

Secondary Egg-Binding Jellies

The individual jelly-covered oocytes are sometimes held together by another type of gelatinous substance (herein referred to as egg-binding jellies) at the time of spawning. When egg-binding jellies are secreted by species with planktic development, they are of a soft consistency that holds eggs together loosely and temporarily in strings or clusters that disperse rapidly in moving water. These strings may persist for longer periods and sink to the bottom as a unit when spawned in still water. This soft type of binding jelly is described in *Calliostoma ligatum* by HADFIELD & STRATHMANN (1990). In trochaceans with benthic embryonic and larval development, binding jellies are of a firmer consistency and are fastened to the substrate, persisting through fertilization and part or all of development. This firm type of binding jelly is characteristic of the attached egg masses of *Calliostoma zizyphinum* (Linnaeus, 1758) and *Cantharidus exasperatus* (Pennant, 1777) (FRETTER & GRAHAM, 1977; FRETTER, 1984).

Egg-binding jellies may be secreted, at least in part, by glandular mantle tissue at the opening of the female urogenital duct into the mantle cavity (FRETTER, 1955, 1984; FRETTER & GRAHAM, 1962). The glandular tissue ranges from a relatively simple thickening in the mantle cavity surrounding the lips of the urogenital opening to a prominent, elongate, protruding papilla. These structures have

been described and/or illustrated for species of *Calliostoma*, *Margarites*, and *Lirularia* that produce egg-binding jellies (FRETTER & GRAHAM, 1962; HADFIELD & STRATHMANN, 1990). As noted above, it is possible that secretions of the hypobranchial gland also contribute to the formation of egg-binding jellies.

Composition and Properties of Primary and Secondary Egg Coverings

There is no documentation of the chemical or physical properties of trochacean egg coverings. UNDERWOOD (1972b) reported that the dispersal of the outer layer of primary egg jelly was retarded in water containing sperm, suggesting a chemical interaction. Secondary egg-binding jellies of differing binding ability, differing densities, and differing persistence times could have a significant influence on the probability of fertilization and on the dispersal of eggs following fertilization and prior to hatching. THOMAS (1992) challenges the assumption that gametes of broadcast spawning invertebrates mix freely in the water column, and her experimental studies of the fluid mechanics of spawning in polychaetes and sea urchins show that gamete buoyancy and gamete clumping can have major effects on fertilization success. The broad range of gamete spawning methods and inferred gamete properties in trochaceans establishes this group as an ideal target for comparative extension of this research.

The primary and secondary gelatinous egg coverings of trochaceans are not homologous with the proteinaceous "capsules" and other egg investments of other prosobranchs (neritomorphs and caenogastropods) and opisthobranchs, which are secreted by distinctive, derived capsule and albumen glands that are part of the terminal reproductive tract. Classifications of "egg capsules" that have not noted this distinction (*e.g.*, AMIO, 1963:table 7) result in categories that are artificial in their phylogenetic constituency.

The Problem of Trochacean Egg Size

Measurements of trochacean egg sizes in the literature are difficult to interpret if the author has not clearly stated what has been measured. Egg measurements may extend beyond the diameter of the yolky egg to include the thickness of the clear envelope surrounding the egg, and the thickness of the inner and outer jelly coatings. Separate measurements of the thicknesses of the various egg coverings are likewise difficult to interpret and compare when measurements have been made after spawning or after contact with seawater. This is because individual layers swell and expand differentially both upon contact with seawater and following fertilization. To minimize the largest source of error, the ranges of egg diameters reported in this review (Table 2) are based exclusively on studies in which authors differentiated between the measurement of the membrane-bounded egg itself and that of the gelatinous egg covering(s).

Sperm

Trochacean sperm are presumed to be of the primitive type (*sensu* RETZIUS, 1906; FRANZÉN, 1956), with a clearly differentiated head (acrosome and nucleus), middle piece, and tail that are traditionally associated with external fertilization. There are few comparative data in the literature, however, and this characterization is extrapolated from ultrastructural studies of members of a single trochid subfamily (Trochinae, tribes Trochini and Gibbulini) (see KOHNERT & STORCH, 1983; KOIKE, 1985; AZEVEDO *et al.*, 1985). While more recent comparative study by John Healy (personal communication) confirms the presence of structurally simple sperm in other trochacean subfamilies, there are several unexpected aberrations. HEALY (1989) documents modified spermatozoa in the primitive eucycline trochid *Calliotropis glyptus* (Watson, 1879), characterized by a deep embedding of the acrosomal complex within the nucleus, effectively eliminating the midpiece region. This is the only report of this form of shortening and invagination in molluscan spermatozoa, although the condition occurs in some polychaetes, arthropods, and echinoderms (see HEALY, 1989:17, for references).

HEALY (1990) reports the presence of dimorphic sperm in the skeneid *Zalipis laseroni* Kershaw, 1958. The presence of both uniflagellate euspermatozoa and multiflagellate paraspermatozoa, conventionally associated with caenogastropods and internal fertilization, provides further evidence of unsuspected diversity within the Trochacea.

Periodicity and Control of Gametogenesis

In trochaceans with seasonal reproduction, the onset of gametogenesis has been correlated both with rising sea temperatures (LASIAK, 1987) and declining sea temperatures (GRANGE, 1976), although it is the seasonal availability of food that is most likely to determine whether gametogenesis can occur. Seasonal ripening of gametes is one mechanism for increasing the probability of reproductive success and is common in marine invertebrates (GIESE, 1959), but it is by no means the exclusive pattern in trochaceans, many of which are continuous breeders. Both patterns may be present within a single trochacean genus or within a single habitat. For example, UNDERWOOD (1972a) has reported both seasonal and continuous breeding in the two co-occurring species of *Gibbula* at Plymouth, England.

There are two kinds of continuous breeding in trochaceans. Some species do not show any seasonal change in the appearance of the gonad and are capable of releasing ripe sperm and eggs continuously throughout the year (UNDERWOOD, 1974). In other species there are reports of synchronized intensified gametogenesis (inferred either from gonadal tissue weight or from histological examination of gonads and determination of proportions of mature gametes) that have been interpreted as indicating spawning peaks (JOSKA & BRANCH, 1983; JOLL, 1980). For example, mature individuals of *Oxystele variegata* (Anton, 1839) un-

Table 2

Classification of trochacean spawning methods. Species are listed in alphabetical order within each of the six categories along with literature citations for each species.

Species	Reference
BROADCAST SPAWNERS (range of egg sizes: 75–200 μm)	
<i>Austrocochlea constricta</i>	Underwood, 1974
<i>Cantharidus coruscans</i>	Simpson, 1977
<i>Gibbula cineraria</i>	Robert, 1902; Lebour, 1937; Fretter & Graham, 1977; Underwood, 1972b
<i>Gibbula divaricata</i>	Bandel, 1982
<i>Gibbula magus</i>	Robert, 1902; Lebour, 1937
<i>Gibbula umbilicalis</i>	Robert, 1902; Lebour, 1937
<i>Monodonta australis</i>	Lasiak, 1987
<i>Monodonta lineata</i>	Lebour, 1937; Desai, 1966; Fretter & Graham, 1977
<i>Oxystele tabularis</i>	Lasiak, 1987
<i>Oxystele variegata</i>	Joska & Branch, 1983; Lasiak, 1987
<i>Subninella undulata</i>	Underwood, 1974
<i>Tegula excavata</i>	Lewis, 1960
<i>Tricolia pullus</i>	Lebour, 1937
<i>Trochus niloticus</i>	Moorhouse, 1932; Heslinga, 1981
<i>Umbonium vestiarium</i>	Berry, 1986
BENTHIC EGG-MASS SPAWNERS (range of egg sizes: 50–200 μm)	
<i>Astrea caelata</i>	Lewis, 1960
<i>Cantharidus exasperatus</i>	Robert, 1902; Lebour, 1937; Fretter & Graham, 1977; Bandel, 1982
<i>Cantharidus japonicus</i>	Amio, 1963
<i>Cantharidus striatus</i>	Robert, 1902; Lebour, 1937
<i>Euchelus gemmatus</i>	Duch, 1969
<i>Gibbula adansonii</i>	Bandel, 1982
<i>Gibbula drepanensis</i>	Bandel, 1982
<i>Gibbula tumida</i>	Gersch, 1936; Lebour, 1937
<i>Lirularia succincta</i>	Hadfield & Strathmann, 1990
<i>Margarella antarctica</i>	Picken, 1979
<i>Margarites helicinus</i>	Thorson, 1935; Lebour, 1937
<i>Margarites groenlandicus</i>	Thorson, 1935; Fretter & Graham, 1977
<i>Margarites marginatus</i>	Hadfield & Strathmann, 1990
<i>Skenea serpuloides</i>	Lebour, 1937; Fretter & Graham, 1977
<i>Tricolia pulloides</i>	Mooers, 1981
<i>Tricolia speciosa</i>	Bandel, 1982
<i>Trochus erythraeus</i>	Gohar & Eisawy, 1963
SPAWNERS OF LOOSELY TACKED EGG STRINGS (range of egg sizes: 170–300 μm)	
<i>Calliostoma papillosum</i>	Robert, 1902; Lebour, 1937; Fretter & Graham, 1977
<i>Calliostoma zizyphinum</i>	Lebour, 1937; Fretter & Graham, 1977
SPAWNERS OF UNATTACHED EGG STRINGS (range of egg sizes: 150–225 μm)	
<i>Calliostoma ligatum</i>	Holyoak, 1988a; Hadfield & Strathmann, 1990
<i>Margarites pupillus</i>	Hadfield & Strathmann, 1990
SHELL BROODERS (range of egg sizes: no data)	
<i>Clanculus bertheloti</i>	Thorson, 1967
<i>Margarites vorticiferus</i>	Lindberg & Dobbertein, 1981
<i>Munditia subquadrata</i>	Burn, 1976
<i>Spectamen verum</i>	Powell, 1979
MANTLE CAVITY BROODERS (egg size: 300 μm)	
<i>Spectamen gerula</i>	Herbert, 1987
<i>Spectamen multistriatum</i>	Herbert, 1987

dergo continuous gametogenesis, but male and female gonadal weights peak in February and again in September–October (JOSKA & BRANCH, 1983). A similar pattern was noted in the subantarctic *Cantharidus* (*Plumbelenchus*) *co-*

ruscans (Hedley, 1916) by SIMPSON (1977), who determined from monthly sampling that the proportion of males and females with ripe gonads peaked in summer (November–January). Continuous maturation of gametes at a low

background level coupled with peak maturation periods, provides a potential bet-hedging mechanism in unpredictable environments.

COLMAN & TYLER (1988) found no significant differences in the proportion of developmental stages in the ovaries of females of the deep-sea (>1000 m) eucyline species *Calliotropis otto* (Philippi, 1844) collected in February, May, July, and August. This suggests the possibility of continuous production of gametes. Data are, however, insufficient for strong inference, and it would certainly be premature to make any generalizations about the presence or absence of reproductive periodicity in deep-sea trochaceans.

Information on the neural and hormonal control and coordination of gametogenesis in trochaceans is not available in either the primary literature or in reviews of endogenous control of gastropod reproduction (e.g., JOOSE, 1979).

SPAWNING METHODS AND BEHAVIORS

Although much of the information on trochacean spawning is anecdotal, there are enough detailed accounts to permit a preliminary classification (Table 2). The table lists representative species and literature citations in each of the categories discussed below.

Broadcast Spawning

Most trochaceans observed to date are broadcast spawners, shedding their gametes into the water column where external fertilization occurs. In broadcasting species, gametes are released in pulses through the right neck lobe as thin streams or milky clouds of sperm and smaller bunches of individual or loosely adhering eggs (Hickman, personal observation; UNDERWOOD, 1972b).

Theoretically, the chances of fertilization in broadcast spawning will be increased (1) if males and females are in close proximity when spawning occurs (aggregation) and (2) if males and females release gametes simultaneously (synchronization). Both mechanisms appear to have evolved independently in different trochacean lineages, although neither mechanism is predominant within the superfamily.

A few broadcasting trochaceans have been observed to aggregate during the spawning season or while engaging in epidemic spawning (DESAI, 1966; SIMPSON, 1977; LASIAK, 1987; HADFIELD & STRATHMANN, 1990). However, actual pairing of males and females during spawning is more common in trochaceans that secrete benthic egg masses or unattached, but initially coherent, egg strings. In the closest form of pairing (contact pairing), the male (sometimes a smaller individual) is stereotypically perched on the female shell to bring the regions of both of the apertures that lie immediately above the exhalant right neck lobes into proximity. Contact pairing has not been reported in broadcasting species.

The timing and coordination of synchronous or epidemic spawning under natural conditions is not well understood. Spawning can be induced under laboratory conditions in some trochacean species by transferring animals to water that is warmer and still (STRATHMANN, 1987). Exogenous physical factors that have been observed to coincide with, but not necessarily trigger, spawning in the field include temperature increase (GERSCH, 1936; DUCROS, 1957; WILLIAMS, 1965; UNDERWOOD, 1972b) and vigorous water movement during rough seas caused by strong onshore winds (GRANGE, 1976). A chemical trigger may be involved in the spawning of gametes in some species that engage in epidemic spawning. Little is known about the endogenous spawning rhythms, although daily, tidal, and lunar periodicities have been reported for some broadcasting species (e.g., BERRY, 1986).

Although synchronization of spawning, like aggregation, is an obvious mechanism for increasing the probability of fertilization in broadcast spawners, there are a number of reports of asynchronous spawning in which gametes are released intermittently as they ripen (e.g., WILLIAMS, 1965; UNDERWOOD, 1972a; LASIAK, 1987).

Theoretical considerations of the fates of gametes that are released into the water emphasize the range of physical effects of fluid turbulence and mixing (DENNY, 1988; DENNY & SHIBATA, 1989) and assume that gametes are neutrally buoyant and individually dispersed. Physical properties of some trochacean gametes deviate from these assumptions in ways that will alter their predicted fates. Recognition herein of a separate category for gametes that are shed as strings or aggregates directs attention to a spawning strategy that should be modeled separately.

Spawning of Benthic Egg Masses

Some trochaceans do not release their eggs into the water column but attach them to the substrate, usually to algae, seagrasses, or the undersides of rocks. In a few instances, individual eggs are surrounded by jelly coating and fixed individually to the substrate [see EISAWY, 1970, for *Trochus dentatus* (Forsk., 1875)], but aggregates or masses are more common.

In the family Trochidae, benthic development within an attached jelly mass is common in members of the primitive subfamilies Eucyclinae and Margaritinae but it should not be interpreted as the primitive mode for the family. Benthic development is most common in high latitude taxa, and it is more probable that this spawning mode has been independently derived numerous times, because it also occurs in temperate, plant-associated trochine species of the tribe Cantharidinae as well as in temperate species of two of the most highly derived trochid subfamilies, Calliostomatinae and Lirulariinae.

The pattern is not necessarily consistent within genera, nor is it always correlated with latitude. There are reports of benthic egg masses for species of *Gibbula* Risso, 1826, from both high and low latitudes [e.g., GERSCH, 1936, for

G. tumida (Montagu, 1803) in the North Sea, and BANDEL, 1982, for *G. drepanensis* (Brugnone, 1873) in the Mediterranean Sea], but the majority of species reported to date are broadcast spawners (FRETTER & GRAHAM, 1977).

Eggs that are spawned in gelatinous strings may be deposited directly onto rocks, algae, or the blades of marine plants in patterns that preserve the form of the original string, such as the sinuous pattern in *Cantharidus striatus* (Linnaeus, 1758) (FRETTER & GRAHAM, 1977:fig. 49), or the spiral pattern in *Gibbula drepanensis* (Brugnone, 1873) (BANDEL, 1982:fig. 11). Alternatively, eggs that are spawned in a soft string of jelly may be molded into a compact mass that is fixed to the substrate by the foot as in *Margarites marginatus* Dall, 1919 [HOLYOAK, 1988b, as *M. helacinus* (Phipps, 1774); HADFIELD & STRATHMANN, 1990]. THORSON (1935) reported similar compact benthic egg masses for *Margarites cinerarius* (Couthouy, 1839) (now commonly regarded as a synonym of *Margarites costalis* Gould, 1841) in northeast Greenland. Most compact masses are relatively shapeless, although GOHAR & EISAWY (1963:fig. I-2) illustrated an inverted cup-shaped mass, with a central cavity, for *Trochus erythraeus* Brocchi, 1821.

There are few direct observations of the formation of egg masses, but DUCH (1969) observed that the looped egg masses of *Euchelus gemmatus* (Gould, 1845) are fixed to the substrate as females crawl in a counter-clockwise direction. PICKEN (1979) observed overlapping egg masses attached to the undersides of rocks by *Margarella antarctica* (Lamy, 1905) at favorable sites in the Orkney Islands. The individual egg masses, which contained as many as 2000 eggs, were deposited in a doughnut shape (PICKEN, 1979:fig. 2A).

Fewer descriptions of egg masses are available for the family Turbinidae. The turbinid *Turbo radiatus* (Gmelin, 1791) is reported to produce a shapeless benthic egg mass (EISAWY & SORIAL, 1974). BANDEL (1982:fig. 12) reported that the tricoliine *Tricolia speciosa* (Mühlfeld, 1824) deposits eggs in simple rounded gelatinous bands on seagrass blades, and MOOERS (1981) observed *Tricolia pulloides* (Carpenter, 1865) producing sinuous jelly-coated ribbons that are consolidated into disc-shaped egg masses and attached to red algae.

Spawning aggregations and contact pairing of individuals (see above) occur primarily in those trochaceans that spawn benthic egg masses. The overlapping egg masses of *Margarella antarctica* described by PICKEN (1979) provide indirect evidence of aggregations of individuals at favorable spawning sites. KOJIMA (1961) described animals of *Cantharidus jessoensis* (Shrenk) as "copulating" in conjunction with the deposition of egg masses on rocks and *Zostera* blades during April and May in Japan. HADFIELD & STRATHMANN (1990) observed pairing of males and females under laboratory conditions during the spawning of benthic egg masses by *Lirularia succincta*. Contact pairing of the small males of *Tricolia variabilis* (Pease, 1861) on the shells of the larger females (WERTZBERGER, 1968; KAY,

1979:fig. 17) occurs throughout the breeding season (October to January) in Hawaii. Males remain on females during this time, and the pairing is not coincidental solely with the act of spawning (Hickman, personal observation). The stereotypic pairing of males and females described by DUCH (1969) for *Euchelus gemmatus* (Gould, 1845) is interesting in the positioning of the smaller male near the left side of the aperture of the female. This is the position of the inhalant current. If sperm are released into the inhalant current, fertilization may occur in the mantle cavity rather than as the eggs are spawned from the right (exhalant) neck lobe.

The most recent morphological classification of gastropod egg masses by SOLIMAN (1987) underestimates the variation in trochaceans by assigning them to two simple categories: shapeless, gelatinous masses, and cup-shaped masses.

Development may proceed at different rates within a single trochacean egg mass, and DUCH (1969) reported more rapid development at the surface of the egg mass than near the center.

Spawning of Unattached Egg Strings

Strings or aggregates of eggs that are spawned from the right neck lobe in an encasing jelly are recognized here as a distinct category that is intermediate between the broadcast spawning of individual eggs and the deposition of attached egg masses.

Spawning of unattached strings or short chains of eggs is part of a unique trochacean variation (described in greater detail below) on the pattern of mixed development (*sensu* PECHENIK, 1979). It is characterized by late hatching of swimming larvae and a brief pelagic phase following predominantly benthic development. It has evolved independently in two trochid subfamilies (Margaritinae and Calliostomatinae) in which other species have totally benthic development and hatch following metamorphosis.

In *Calliostoma ligatum*, unattached chains have been described by HUNT (1980), HOLYOAK (1988a), and HADFIELD & STRATHMANN (1990). Although the egg-binding jelly breaks down rapidly in moving water, egg strings spawned in still water remain together during fertilization and sink to the bottom and undergo early embryonic development as a unit. As noted above, pairing of males and females during spawning is not uncommon. HADFIELD & STRATHMANN (1990) noted that sperm had penetrated both the egg-binding jelly and the individual jelly coatings in freshly collected eggs from a female that was paired with a male during spawning.

BANDEL (1982) reported the spawning of free-floating egg strings by *Calliostoma laugieri* Payraudeau, 1826, and the spawning of gelatinous floating aggregates of 2–10 eggs by *C. granulatum* (Born, 1778). In both species, Bandel noted that hatching occurs before metamorphosis and that the veliger is capable of swimming for short distances.

RAMÓN (1990) also reported *C. granulatum* spawning unattached egg strings ("eggs were attached in long ribbons," which "remained joined together in amorphous masses that came to rest on the bottom"), although she did not observe any swimming between hatching and loss of the velum. Spawning of eggs in short chains also occurs in *Margarites pupillus* according to HADFIELD & STRATHMANN (1990).

Although it is tempting to classify species that shed their eggs into the water without fixing them to the substrate as broadcast spawners, the cohesiveness of the eggs at the time of fertilization, their negative buoyancy and settlement to the substrate, and their adherence to one another after fertilization is fundamentally different from the situation in broadcasting. Furthermore, the time of hatching has been shifted to very late in development. *Calliostoma ligatum* does not hatch until after torsion is completed (HOLYOAK, 1988a), whereas the typical trochacean with planktic development hatches as a trochophore or early, pre-torsional veliger.

Spawning of Loosely Tacked Egg Strings

An additional category forms a link between the spawning of unattached strings of eggs and those that are firmly fixed to the substrate. In this category, a cylindrical, gelatinous string of unattached eggs is tacked to the substrate at intervals by the front end of the foot. The long, partially floating string of eggs of *Calliostoma zizyphinum* (Linnaeus, 1758) illustrated by FRETTER & GRAHAM (1977:fig. 56) appears to be tacked to the substrate at only three points. In contrast to the *Calliostoma* species that spawn unattached strings and hatch as late veligers, *C. zizyphinum* hatches following metamorphosis (ROBERT, 1902; LEBOUR, 1936; FRETTER & GRAHAM, 1977).

BANDEL (1982:fig. 13) illustrated the egg string of *Calliostoma zizyphinum* as circular in cross-section, and reported individual strings that reached a meter in length and contained 1500 eggs spawned at a rate of 10 to 35 per minute.

Brooding

Brooding is not common in trochaceans, but it occurs throughout the superfamily, in primitive as well as highly derived groups. It occurs principally in species from high latitudes. ROBERTSON (1985b) tabulated reports of actual or suspected brooding in primitive marine gastropods. There are documented instances of protection of developing embryos and larvae in three trochid subfamilies (Margaritinae, Trochinae, and Solariellinae) and one turbinid subfamily (Liotiinae).

LINDBERG & DOBBERTEN (1981) described umbilical brooding in females of the primitive margaritine trochid *Margarites vorticiferus* (Dall, 1873). Brooding in this species is coupled with sexual dimorphism in the shell, with females having a broader umbilical cavity. DOBBERTEN & ELLMORE (1986) further observed that secretion of the

postlarval shell in this species begins while individuals are still confined to the brood space, which they cited as evidence of precocious appearance of adult traits.

THORSON (1967) reported brood protection within the spiral grooves on the bases of both male and female shells of *Clanculus bertheloti* d'Orbigny, 1839. An earlier illustration, from Thorson's 1950 Christmas card, of larvae covered with a thin mucus layer, was reproduced by PURCHON (1968:fig. 101). Climo in POWELL (1979:64) reported umbilical brooding in a derived solarielline, *Spectamen verum* (Powell, 1937), and HAYWARD & GRACE (1981:fig. 3) subsequently illustrated a specimen with a brood. BURN (1976) illustrated an individual of the liotiine *Munditia subquadrata* (Tenison-Woods, 1878) with a mass of developing embryos in the umbilicus.

HERBERT (1987) discovered the first instances of trochacean brooding of embryos and larvae within the mantle cavity in two South African solarielline species, *Spectamen gerula* Herbert, 1987, and *S. multistriatum* (Thiele, 1925).

Ovoviviparity

True ovoviviparity, retention of developing embryos and larvae within the oviduct, is unknown in trochaceans. The nature of the dimorphism in shell size and shape in two high-latitude trocholine species, *Tricola gabiniana* (Cotton & Godfrey, 1938) and *T. rosea* (Angas, 1867), led ROBERTSON (1985b) to suggest the possibility of brooding within the mantle cavity or the oviduct. ARNAUD (1972) reported seeing "nombreux jeunes" through the translucent spire of specimens of *Margarites refulgens* (Smith, 1907) from the Antarctic. However, specimens provided by Arnaud to D. R. Lindberg do not have translucent spires, and it is uncertain what Arnaud observed.

Ovoviviparity requires a reliable method of sperm transfer to the female. It is highly unlikely to occur in species that do not engage in contact pairing and that do not have a penis or analogous structure for sperm transfer. The fact that there is direct and stereotypic contact of individuals in some trochaceans, however, suggests that sperm transfer and internal fertilization could occur. The as yet poorly understood elaborations of the male right neck lobe reported above may represent an evolutionary step in the direction of internal fertilization.

SPAWNING PERIODICITY

Seasonal Periodicity

In trochaceans with seasonal spawning, the periodicity should be related to an underlying seasonal periodicity in gametogenesis, discussed above. Few reports provide direct observations of trochacean spawning periodicity. Determination of spawning time usually is based on indirect evidence, such as seasonal changes in the condition of the gonads, the time of appearance of egg masses, or recruitment of newly settled juveniles in an environment (e.g., UNDERWOOD, 1974; SIMPSON, 1977; JOLL, 1980; MOOERS,

1981; JOSKA & BRANCH, 1983; LASIAK, 1987). More indirectly, estimates of spawning time have been extrapolated from seasonal size-frequency data [e.g., WELLS & KEESING, 1987, for *Cantharidus pulcherrimus* (Wood, 1828)].

The ease with which spawning can be induced under laboratory conditions may provide a more precise indication of when spawning is likely to occur under natural conditions. For example, HADFIELD & STRATHMANN (1990) were unable to induce spawning in *Margarites pupillus* collected in May, early June, and July, whereas they were successful with animals collected between 12 and 26 June in Washington state.

Although sampling for the presence of eggs in the plankton provides a direct method of monitoring spawning activity in the field, this is probably not practicable unless populations are extremely dense and reproductive output extremely high. BERRY (1987) used daily plankton egg counts over a 79-day period of observation to estimate the reproductive output of individuals and the entire population of *Umbonium vestiarium* (Linnaeus, 1758) on a Malaysian sand flat.

Unfortunately, single records of gonad condition or egg masses spawned in aquaria have been tabulated and published as reports of "breeding seasons" (e.g., BOVARD & OSTERUD, 1918; HEWATT, 1938). Breeding-season data reported in faunal manuals must be interpreted with caution.

Diurnal, Tidal, and Lunar Periodicities

There are very few data on finer-scale spawning periodicities. GRANGE (1976) found no relationship between spawning and time of day (night or day), state of the tides (position in the tidal cycle), or time of month (position in the lunar cycle) in New Zealand trochids and turbinids.

Many marine invertebrate groups show a pattern of nighttime spawning on spring tides (KORRINGA, 1957; NAYLOR, 1976) that has been attributed in adaptational terms to nocturnal safety from predation and the greater dispersal potential of spring tides (e.g., BERRY, 1986). HESLINGA & HILLMAN (1981) reported a 28-day periodicity of spring tide spawning in *Trochus niloticus* in Palau.

In spite of the alleged advantage of releasing gametes on nocturnal spring tides, the best documented fine-scale spawning periodicity in a trochacean is the midday spawning of *Umbonium vestiarium* (Linnaeus, 1758) on high or falling neap tides (BERRY, 1986). *Umbonium* is classified in a highly derived subfamily and tribe of trochids that are specialized for infaunal suspension feeding (HICKMAN, 1985; HICKMAN & MCLEAN, 1990). *Umbonium vestiarium* occurs at unusually high densities (12,000/m²) on tropical intertidal sandflats, where it comprises >99% of the intertidal biomass (BERRY, 1986). It undergoes the most rapid development reported for any trochacean, settling and metamorphosing 36–48 hr after fertilization (BERRY, 1986). It is also an annual species with one discrete period of spawning and recruitment each year (BERRY & ZAMRI,

1983; BERRY, 1987). The adaptive advantages of a reproductive pattern that limits dispersal, promotes larval settlement in the environment of their origin, and favors settlement of briefly pelagic larvae at times of maximum submergence in quiet water is discussed by NAYLOR (1976) and BERRY (1986).

DEVELOPMENTAL STAGES AND TIMING

The length of time between fertilization and metamorphosis (as a benthic juvenile capable of crawling, feeding, and retracting into its shell) of trochaceans varies from 2 or 3 days (HESLINGA, 1981; BERRY, 1986) to 28 days (HADFIELD & STRATHMANN, 1990). Developmental times can be altered under laboratory conditions and generally are longer at lower temperatures and higher latitudes. However, rate of development is not uniform throughout development. Prolonged developmental time results principally from delayed settling and/or delayed metamorphosis. In the tropical *Trochus niloticus*, HESLINGA (1981) found that settlement could be delayed for 7 days and metamorphosis for 13 days in the absence of algal inducers. Delay of settlement is potentially significant to dispersal because of the additional time that larvae spend in the water column.

The major stages and events in trochacean embryonic and larval development are summarized in Table 3, and the stages are illustrated in Figure 2. The major stages, for the purpose of this discussion, are: (1) fertilized egg, (2) two-cell cleavage through blastula, (3) gastrula, (4) trochophore, (5) pre-torsional veliger, (6) post-torsional veliger, (7) swimming-crawling demersal veliger, and (8) fully metamorphosed juvenile. These stages are arbitrary, but useful principally because the onset of each is marked by the appearance of a feature (e.g., development of the prototroch or the velum) that is relatively easily recognized, and because the developing animal has a characteristic overall appearance and organizational uniformity throughout each stage even though there may be many important developmental events occurring within each stage.

The corresponding developmental events that mark the beginning of each of the above stages are: (1) fertilization, (2) cleavage, (3) gastrulation, (4) prototroch formation, (5) velum formation, (6) torsion, (7) settlement, and (8) metamorphosis. The order of these main events is the same in all trochaceans, but their timing varies. There are many other events that occur within stages, and there is some variation in the order of appearance of features. The most important events occurring within developmental stages are listed in Table 3.

In evolutionary terms, hatching is the most labile event in trochacean development, and its significance will be discussed in greater detail below. Variation in hatching time in six trochaceans with different developmental patterns is illustrated in Figure 3. What is important about hatching is not how long it takes, which is strongly correlated with temperature both across and within species,

Table 3

Chronological sequence of trochacean developmental stages and events. Early embryonic development and larval development are subdivided into stages. The event characterizing the onset of each stage is listed first, followed by events that usually occur within the stage, although not necessarily in the order listed. The variable events of hatching and early settlement are inserted in parentheses at points where they can occur in the chronological sequence.

Stage	Event
EARLY EMBRYONIC DEVELOPMENT	
Fertilized egg	fertilization: penetration of jelly coating(s) and egg membrane by sperm swelling of egg and associated coatings hardening of jelly coating polar body formation and extrusion
Two-cell through blastula	cleavage , with increasingly asynchronous division of macromeres and micromeres polar flattening of blastula
Gastrula	formation of blastopore and gastrulation , overgrowth of blastula by ectoderm appearance of locomotor cilia beginning of ciliary beating, with increasing coordination of beat beginning of rotation of gastrula within egg membrane differentiation of ectoderm into pretrochal, trochal, and posttrochal cells increasing constriction of blastopore
LARVAL DEVELOPMENT	
Trochophore	prototroch formation by enlargement of trochal cells and elongation of trochal cilia appearance of shell gland appearance of foot rudiment closure of blastopore invagination of stomodaeum (HATCHING) appearance of first shell material ano-pedal flexure
Pre-torsional veliger	velum formation , through enlargement of prototroch (HATCHING) development of two distinct velar lobes appearance of opercular rudiment and operculum appearance of mantle fold and mantle cavity appearance of digestive gland
Post-torsional veliger	torsion (first 90 degrees) (HATCHING) completion of torsion (second 90 degrees) (EARLY SETTLEMENT) (HATCHING) asymmetric deformation of unmineralized larval shell mineralization of larval shell first attempts to retract into shell

Table 3

Continued.

Stage	Event
	reduction of velum and elongation of foot appearance of mouth appearance of radula sac (and radula?) appearance of digitate cephalic tentacles appearance of epipodial tentacles appearance of eyes
Swimming-crawling stage	settlement or end of exclusively pelagic period attempted crawling and retraction into shell; attempted balancing of shell
Juvenile snail	metamorphosis with loss of velum and full development of ability to crawl, feed, and retract into shell (HATCHING)

but the fact that its position is not fixed within the developmental sequence (Table 3 and Figure 3). In species that have exclusively benthic development (e.g., *Margarites marginatus*), by-passing a planktic larval stage, hatching occurs after metamorphosis (defined here as loss of the velum and assumption of a crawling and feeding mode of life). Across species that have a lecithotrophic planktic stage, there is no fixed point at which larvae become free: hatching may occur as early as the trochophore stage (e.g., *Umbonium vestiarium*, *Trochus niloticus*, and many other species) or as late as the post-torsional veliger stage (e.g., *Calliostoma ligatum*). This is in marked contrast to planktotrophic caenogastropods, which hatch from capsules as well-developed post-torsional veligers (FRETTER & GRAHAM, 1962).

Settlement is also a variable event in trochacean development, occurring as early as the end of the first 90 degrees of torsion (e.g., *Gibbula cineraria*). At this stage of development, some other trochaceans have not yet hatched and begun their planktic stage. Completion of the second half of torsion after settlement may be primitive, because it is also reported in haliotids (CROFTS, 1937). Even trochaceans that settle immediately following the completion of torsion are leaving the water column at the stage of development when the typical caenogastropod veliger is hatching and beginning its planktic larval life. Settlement is not always easy to recognize as a discrete event. Larvae gradually may spend less time swimming and more time at or near the bottom during the later stages of torsion. In this swimming-crawling stage, discussed in greater detail below, the larva is no longer capable of efficient swimming and not yet capable of retracting, crawling, or balancing the shell over the head and foot (Figure 2M).

Fertilization

Sperm penetration of the egg membrane is not readily observed as a discrete event, and the time of fertilization

is usually inferred from visible changes in the egg and its associated structures (Figure 2A, B), or from the onset of cleavage.

In species that pair while the female deposits a benthic egg mass or extrudes an unattached egg string, fertilization apparently occurs rapidly. HOLYOAK (1988b) observed active sperm both within the egg-binding jelly and within the jelly coats of individual eggs following their deposition on the substrate by *Margarites marginatus* (as *M. helacinus*). HADFIELD & STRATHMANN (1990) reported that unattached strings of eggs extruded by *Calliostoma ligatum* were fertilized at the time of examination, immediately following collection from individuals that had been paired as the eggs emerged from the mantle cavity of the female.

Fertilization may be equally rapid in broadcasting trochaceans, especially those with synchronized spawning. HESLINGA (1981) interpreted the increase in egg diameter that occurred within a few minutes of spawning as indicative of fertilization in *Trochus niloticus*. UNDERWOOD (1972b) noted that a swelling confined to the outer layer of the jelly coat of eggs broadcast by *Gibbula cineraria* was impervious to sperm penetration and was a pre-fertilization event. Fertilization occurred only after the outer layer had dispersed. Accordingly, UNDERWOOD (1972b) defined disappearance of the outer jelly coats as the event marking fertilization.

Cleavage and the Early Stages of Cell Differentiation

The most detailed account of trochacean cleavage and the fate of cell lineages is that of ROBERT (1902) for *Gibbula magus* (as *Trochus magus* Linnaeus, 1758). Formation and extrusion of the first and second polar body follow closely on fertilization, and the first cleavage begins soon after appearance of the second polar body. Reports of the times of the first cleavage fall between 1 and 5.6 hr after inferred fertilization (DESAI, 1966; DUCH, 1969; UNDERWOOD, 1972b; MOOERS, 1981; HOLYOAK, 1988a, b). Few reports continue in detail beyond the first two meridional cleavages.

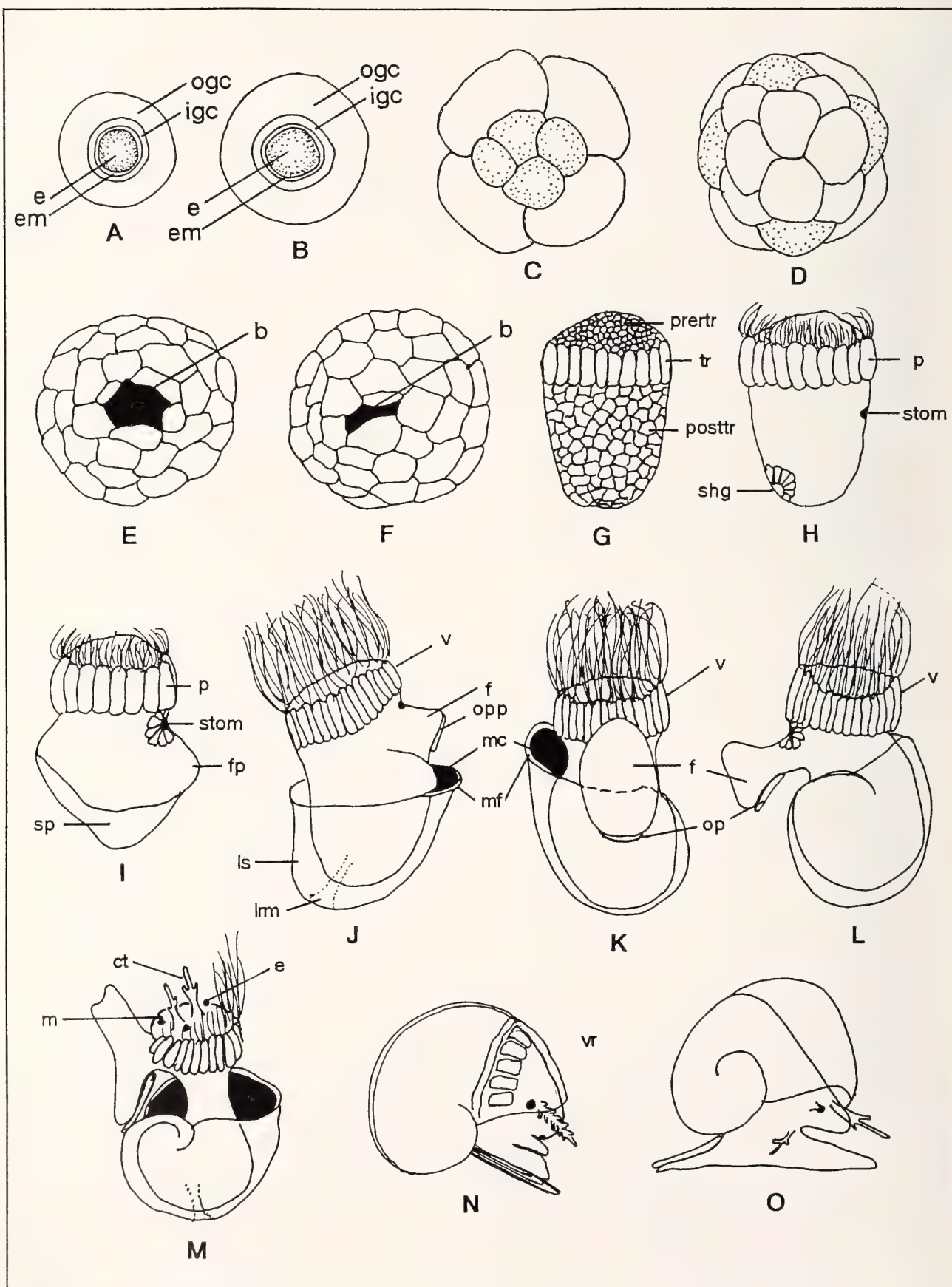
Subsequent cleavage follows the classical spiralian pattern, and there is nothing unique to trochaceans, gastropods, or even mollusks, about the progression of alternating dextrotropic and laeotropic divisions leading to formation of the blastula. After the first two equal and meridional cleavages, spiral cleavage begins with the dextrotropic third cleavage, which produces an asymmetric 8-cell stage with large macromeres and small micromeres (Figure 2C). UNDERWOOD (1972b) is the only recent author to describe cleavage in any detail as far as the fifth cleavage. He noted asynchrony of division of the macromeres and micromeres at the fourth cleavage (producing a transient 12-cell stage

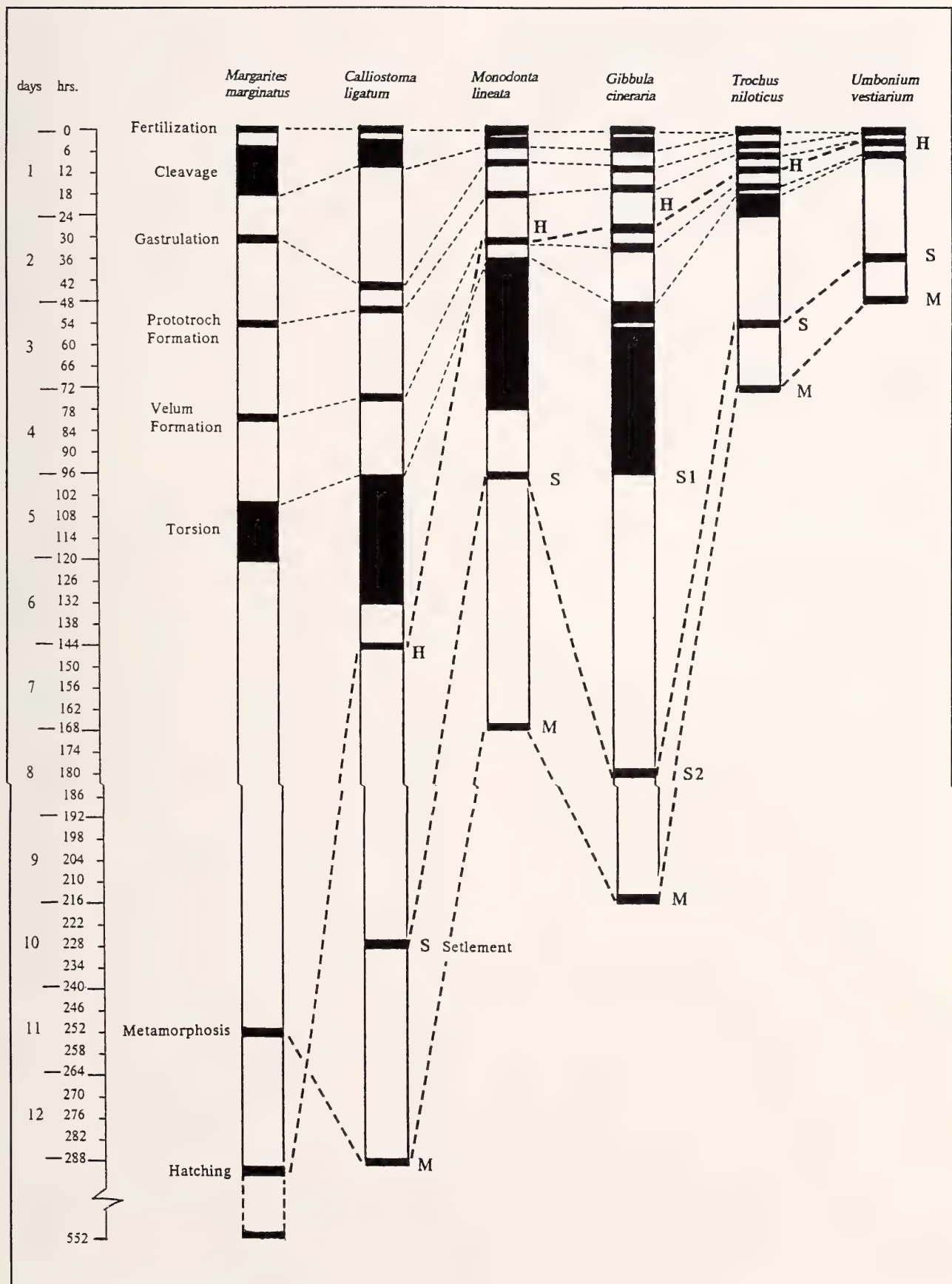
Figure 2

Trochacean developmental stages. A. Egg prior to spawning: e, egg; em, egg membrane; igc, inner gelatinous coating; ogc, outer gelatinous coating. B. Unfertilized egg after swelling in seawater. C. Fertilized egg at the 8-cell stage, after the third cleavage (the first spiral, dextrotropic cleavage), with first quartet of micromeres shaded. D. Egg at the 16-cell stage, after the fourth cleavage (laeotropic), with the second quartet of micromeres shaded. E. Early gastrula, following epiboly, with wide open blastopore (b). F. Late gastrula, with blastopore nearly closed. G. Early trochophore larva showing relative cell sizes and shapes: pretr, pretrochal cells; tr, trochal cells; and posttr, posttrochal cells. H. Early trochophore larva: p, ciliated prototroch; shg, position of shell gland invagination; stom, stomodaeal invagination. I. Late trochophore with shell primordium (sp) secreted by shell gland and foot primordium (fp). J. Pre-torsional veliger from right side: v, velum; f, foot; mc, mantle cavity; mf, mantle fold; opp, opercular primordium; lrm, larval retractor muscle; ls, larval shell. K. Planktic veliger in ventral view after first 90 degrees of torsion: f, foot; op, operculum. L. Planktic veliger in left lateral view after first 90 degrees of torsion. M. Extended benthic veliger in left lateral view after first 90 degrees of torsion, with mantle cavity on the right side: m, mouth; ct, cephalic tentacle, e, eye. N. Partially metamorphosed and partially retracted demersal veliger in right lateral view at the completion of torsion: vr, velar remains. O. Fully metamorphosed, benthic juvenile in right lateral view.

Figure 3

Comparative development of six trochacean gastropods. The events of fertilization, cleavage, gastrulation, prototroch formation, appearance of the trochophore stage, hatching, appearance of the veliger stage, torsion, settlement, and metamorphosis are depicted by black bands of width corresponding to the reports of time or range of time of observations reported in the literature. The onset of events is correlated by dashed lines. Heavier dashed lines are used to correlate hatching (H), settlement (S), and metamorphosis (M) to emphasize the variation in timing and order of these three events. Species are arranged to emphasize the shift in hatching time to progressively earlier stages of development: the hatching time line crosses the time line of velum formation between *Monodonta lineata* and *Gibbula cineraria*. Total development time is correlated with temperature and latitude and is less significant than the order of events. Sources of data are: *Margarites marginatus* (HOLYOAK, 1988b; HADFIELD & STRATHMANN, 1990); *Calliostoma ligatum* (HOLYOAK, 1988a, HADFIELD & STRATHMANN, 1990); *Monodonta lineata* (DESAI, 1966); *Gibbula cineraria* (UNDERWOOD, 1972b); *Trochus niloticus* (HESLINGA, 1981); *Umbonium vestiarium* (BERRY, 1986).





before arriving at the 16-cell stage [Figure 2D]), followed by a staggered division of the micromeres during the fifth cleavage, giving rise to transient 20-, 24-, and 28-cell stages before arriving at the 32-cell stage. Beyond the fifth cleavage, the increasing asynchrony of division of the micromeres makes cleavage more difficult to follow through the sixth cleavage. Polar flattening occurs shortly before the onset of gastrulation.

Gastrulation and the Gastrula Stage

The most detailed description of gastrulation in a trochacean is also that of ROBERT (1902). Gastrulation occurs by epiboly, with the enclosure of the macromeres by the micromeres. The blastopore is initially wide and circular (Figure 2E), becoming narrow and slit-like in the late gastrula (Figure 2F). Locomotor cilia appear during this stage, closely followed by the initiation of irregular ciliary beating and then the increasing coordination of the beat. Rotation of the gastrula within the egg membrane has been observed as early as 9 hr after fertilization (HESLINGA, 1981). Clear differentiation of the ectoderm into pretrochal, trochal and posttrochal cells begins during this stage, and it is the subsequent elongation of the trochal cilia and formation of the prototroch that identifies the beginning of the trochophore stage (Figure 2G).

Prototroch Formation and the Trochophore Stage

The familiar trochophore larva (Figure 2H) is recognized by enlargement of the trochal cells, elongation of cilia, and formation of the prototroch. Several important events occur during the trochophore stage, including appearance of the shell gland, the foot primordium, and the first secretion of shell material (Figure 2H, I). The blastopore closes, and the stomodaeum (precursor of the mouth, pharynx, and esophagus) forms by invagination (Figure 2H, I). This is the earliest stage of development during which hatching has been reported. Hatching and the assumption of planktic life during the trochophore stage are reported for both tropical species (*e.g.*, HESLINGA, 1981; BERRY, 1986) and temperate species (*e.g.*, UNDERWOOD, 1972b). In species that hatch as trochophores, the first thin transparent layer of unmineralized, organic, embryonic shell material (secreted by the shell gland) appears immediately after hatching (Figure 2I). The process of shell formation begins during the subsequent veliger stage following formation of the mantle fold (Figure 2J). Anopodal flexure also occurs during the trochophore stage (DESAI, 1966), bringing the rectum into a ventral position beneath the stomodaeum and developing foot.

Velum Formation and the Pre-Torsional Veliger Stage

The velum develops by enlargement of the prototroch, anterior migration of cells, and development of longer and

more numerous cilia on the anterior row of cells. The larva now can be considered a pre-torsional veliger. Formation of the velum may occur either after hatching or within the egg membrane. The trochacean velum, in contrast to that of caenogastropods, is a relatively small and simple structure, highly effective in locomotion but never hypertrophied and elaborated as a multi-lobed suspension-feeding structure with addition of a postoral ciliary band and food groove.

As pre-torsional development continues (Figure 2J), the opercular primordium and operculum appear, as well as the mantle fold, the mantle cavity primordium, and the distinctive cells of the digestive gland. During this stage, a small, bilaterally symmetrical, cup-shaped shell is formed. In species that hatch as early veligers, the organic (unmineralized), cup-shaped shell may be well developed at the time of hatching. Torsion of the visceral mass cannot begin until after the larval retractor muscle is developed and inserted on the shell.

Torsion and the Post-Torsional Veliger Stage

The most detailed description of trochacean torsion is that of CROFTS (1955) for *Calliostoma zizyphinum*, a species in which the whole of torsion occurs within the egg covering prior to hatching. Earlier accounts of torsion in trochids were published by ROBERT (1899, 1902). Croft's account emphasizes the development of the larval retractor muscle and its behavior during torsion.

The first 90 degrees of torsion is alleged to be rapid (approximately 4–8 hr) and is the result of contraction of the larval retractor muscle, shifting the axis of the cephalopodal mass counter-clockwise, when viewed from below (ventral) relative to the visceral mass and displacing the mantle cavity primordium and anterior (growing margin) of the shell to the right side (Figure 2K, L). In trochaceans the onset of torsion is reported to vary from 14 hr (HESLINGA, 1981, for *Trochus niloticus*) to more than 100 hr (HOLYOAK, 1988b; HADFIELD & STRATHMANN, 1990), although few studies have followed development closely enough to pinpoint the initiation or progress of the event.

The remaining 90 degrees of torsion, bringing the mantle cavity primordium and growing margin of the shell to an anterior position, is less rapid (on the order of 30 to 50 hr) and appears to take place by differential growth rather than muscle contraction (CROFTS, 1955). BANDEL (1982) makes no reference to two phases of torsion and attributes the entire process to differential growth of epithelial cells. Other important developmental events during the second half of larval torsion include continued development of the larval shell, and appearances of the mouth, radula sac (and radula in some species), ctenidial primordium, digitate cephalic tentacles, epipodial tentacles, and eyes. The foot also elongates, and the first attempts are made, late in the stage, to retract into the shell (Figure 2L). At this stage, however, the mantle cavity is still insufficiently developed

to accommodate the animal, and full retraction will not be possible until after metamorphosis, including resorption of the left larval retractor and formation of the columellar muscle from the right mesodermal band. The second half of torsion may take place either in the water column or on the bottom during the swimming-attempted crawling stage.

Hatching and the beginning of a planktic stage may be delayed until after the completion of torsion in some trochaceans such as *Calliostoma ligatum* (HOLYOAK, 1988a; HADFIELD & STRATHMANN, 1990), while in others, such as *Gibbula cineraria*, reduction of the velum, settlement, and awkward attempts at crawling have already begun before torsion is completed (UNDERWOOD, 1972b). Asymmetric mechanical deformation of the larval shell occurs after torsion is complete, transforming the cup-shaped shell into a trochispiral form. Mineralization of the shell follows mechanical deformation. The post-torsional veliger of *C. ligatum* at the time of hatching has a well-developed, mineralized shell, foot, and operculum (Figure 4).

Reduction of the velum and the processes of settlement and metamorphosis may be prolonged or delayed. HADFIELD & STRATHMANN (1990) report that some post-torsional veligers of *Margarites pupillus* were capable of spending equal amounts of time swimming and crawling a month after fertilization. The post-torsional veliger stage also may be prolonged in species that undergo a slow process of benthic development before hatching as adults, as in *Margarites marginatus* (HADFIELD & STRATHMANN, 1990).

Settlement and the Swimming-Crawling Stage

Settlement is not always a distinct event in trochaceans. Reduction of the velum and development of the foot as an efficient crawling structure may occur gradually during and after torsion. A veliger that swims actively in the pre-torsional stage may spend increasingly greater amounts of time on the bottom (motionless) or near the bottom (in less well coordinated, jerky swimming) during the later stages of torsion. Accordingly, settlement and the swimming-attempted crawling stage mark the end of an exclusively pelagic period (the period in which dispersal over substantial distances is most likely to occur). During this stage animals attempt retractions into the shell (Figure 2N) and normal locomotion, but they are unable to adhere effectively to the substrate with the sole of the foot, and they do not yet have an adequately developed columellar muscle and muscle coordination to pull the shell over the cephalopodal mass (UNDERWOOD, 1972b).

It is not certain whether animals in this premetamorphic state are ever capable of feeding. UNDERWOOD (1972b) noted that the mouths of individuals of *Gibbula cineraria* were open and making searching movements during this stage, but he was unable to find a radula, even in fully metamorphosed individuals. FRETTER (1967) observed that the late veliger of *Haliotis* (a member of the trochacean



Figure 4

Post-torsional veliger of *Calliostoma ligatum* (Gould, 1849) at the time of hatching, viewed from the right side showing velum, foot, and well-developed operculum. Micrograph provided by M. G. Hadfield and M. F. Strathmann.

sister group Pleurotomariacea) is "scraping the rock surface for food." DESAI (1966) first observed a functional odontophore and radula in *Monodonta lineata* one week after metamorphosis. It is not necessary that a radula be present in order to ingest small food particles, and the movements that have been observed strongly suggest that the "swimming-crawling stage" is one in which some benthic feeding occurs. A functional radula is present in some species that hatch immediately after metamorphosis, and DUCH (1969) reported *Euchelus gemmatus* ripping open the egg covering with its radula.

Trochaceans live on and in a wide variety of substrates, and it is assumed that chemical cues are involved in the induction of settlement and metamorphosis of some, if not all, species. HESLINGA (1981) reports that settlement in *Trochus niloticus* can be induced by a primary algal film on culture dishes and by the coralline alga *Porolithon* sp., but nothing is known of the actual chemistry of the inducers.

Likewise, nothing is known of the mechanics of chemosensory reception in trochacean settlement and metamorphosis. TRAPIDO-ROSENTHAL & MORSE (1986) have shown that regulation of settlement and metamorphic morphogenesis in *Haliotis rufescens* Swainson, 1822, is highly complex. Their work provides a general model of the level of complexity that we might expect in those trochaceans that are substrate-specific. It also provides an indication of the amount of work required to achieve even a rudimentary

comparative understanding of the interactions between larvae and substrates in trochacean recruitment.

Metamorphosis and the Early Juvenile Stage

Definition of the term "metamorphosis" has been debated at length in the literature on marine invertebrate development. For several excellent discussions of the terminology of molluscan metamorphosis, see BONAR (1978) and TURNER *et al.* (1986). Metamorphosis is usually defined *ecologically* as an event that is restricted to free-swimming larval stages (GIESE & PEARSE, 1974:8). I here define metamorphosis *morphologically* as an accelerated sequence of structural losses and additions that transform the veliger into a juvenile. The most important is the loss of the velum, which commits the veliger to metamorphosis. Loss of the velum in trochaceans is accompanied by events that must be inferred from behavioral observations, in the absence of any direct accounts of metamorphogenesis. These include (1) enlargement of the foot and rapid organization of pedal musculature and neuromuscular coordination for crawling locomotion, (2) development of the columellar muscle (from the post-torsional right mesodermal band) for balancing the shell over the cephalopedal mass and for full retraction of the animal into the shell, and (3) development of the radula and complex buccal musculature for feeding. By this definition, metamorphosis is an event in the life history of all trochaceans, whether it occurs at the end of a free-swimming larval stage or at the end of benthic development just prior to hatching. The morphological definition recognizes homology in a set of larval features that are abolished and a set of juvenile features that are established during the metamorphogenetic transition.

Furthermore, the ecological distinction (GIESE & PEARSE, 1974) between "larvae" (planktic) and "embryos" (brooded or encapsulated) has no morphological basis in trochaceans. A veliger is morphologically a veliger, whether it is a larva or an embryo. It also follows that "direct development" in the classical morphological and embryological sense (CHIA, 1974) does not occur in trochaceans. The ecological definition of "direct development" as elimination of a *free-swimming larval stage* (THORSON, 1936, 1950; MILEIKOVSKY, 1971; WEBBER, 1977) can lead to false inferences of what it is that has been eliminated. In the classical morphological sense, direct development involves evolutionary loss of distinct larval stages, with direct differentiation of adult morphology ("ametamorphic development," *sensu* BONAR [1978]). Application of the term "direct development" to trochacean gastropods has been misinterpreted in the literature as *loss* of the veliger stage (*e.g.*, MATSUDA, 1987:114).

Variation in the length of time to metamorphosis in trochaceans is perhaps the most obvious feature of Figure 3. However, duration of development is strongly correlated with latitude and temperature, and is less significant than the observations that (1) none of the species has lost or gained developmental stages, (2) none of the species has

become ametamorphic, and (3) the timing of hatching and metamorphosis have crossed lines and changed their positions within the developmental sequence.

An early postmetamorphic juvenile (Figure 2O) does not yet have the full complement of adult epipodial structures, and it is uncertain how soon the inhalant and exhalant neck lobes develop to aid in circulation of water through the mantle cavity.

What are the magnitude and range of metamorphogenetic change in trochaceans? Is this richly compressed series of events an untapped source of data that can be mapped onto phylogenetic hypotheses to infer major pathways of evolutionary change? HADFIELD (1978) used a comparison of molluscan metamorphosis and anuran metamorphosis to pose some exciting questions for molluscan developmental biology. These questions are equally exciting in their evolutionary implications. Metamorphosis currently is best documented in opisthobranchs, and especially nudibranchs, where the magnitude of change is greatest (see BONAR, 1978, and references therein). Comparable studies of prosobranchs are overdue, and the range of observed variation in trochacean development makes this primitive prosobranch superfamily a promising target for detailed analysis.

HETEROCHRONY AND THE EVOLUTIONARY SIGNIFICANCE OF HATCHING TIME

In an evolutionary sense, hatching is a key event in trochacean development, because change in the time of hatching has produced novel developmental patterns. The significance of hatching has been misunderstood. Some theoretical evolutionary considerations have focused on the importance of changes or disruptions in patterns of metamorphosis (*e.g.*, MATSUDA, 1987). As stated above, it has been wrongly assumed that the significance of hatching as an adult lies in the elimination of larval stages and of metamorphosis as an event.

Other theoretical considerations have attached special evolutionary significance to whether larvae are planktic or benthic (*e.g.*, SCHELTEMA, 1978) and, more specifically, whether planktic larvae are feeding or nonfeeding (*e.g.*, STRATHMANN, 1978; JABLONSKI & LUTZ, 1980, 1983). JABLONSKI & LUTZ (1983) rejected the term "direct development" with reference to prosobranchs, but their dichotomy between planktotrophic and nonplanktotrophic development forces all trochaceans into the same category regardless of where they develop, how long they spend in various developmental stages, or at what point hatching takes place relative to metamorphosis.

Hatching that follows metamorphosis dictates that development will be exclusively benthic. Variation in earlier times of hatching, however, provides opportunities for mixing benthic and planktic development in several different ways. When eggs that have been in the plankton since fertilization hatch in the trochophore or early veliger stage, development may proceed in one of two directions: (1)

remaining in the plankton as an actively swimming, phototropic larva that may prolong its life in the water column or (2) settling and completing a portion of its late larval development on or near the bottom. The demersal larva retains its ability to swim and also may experience selection for delaying metamorphosis until a suitable substrate has been located.

Perhaps the most poorly appreciated and poorly understood pattern of mixing benthic and planktic development is seen in the late (post-torsional) hatching of veliger larvae in calliostomatine gastropods that spawn egg strings. The calliostomatine egg string, which may be either free or tacked loosely to the substrate, provides the potential for a substantial period of enclosed development at the bottom, followed by a planktic stage, before returning to the bottom for a period of demersal development before the velum is lost.

Although post-torsional hatching of veliger larvae is unusual in trochaceans, it is the typical pattern of development in planktotrophic caenogastropods, where relatively long-lived veligers with elaborate velar structure hatch and move into the plankton only after torsion has taken place. Calliostomatine gastropods are highly derived trochaceans, and the evolution of post-torsional hatching probably happened independently in this subfamily. The range of variation and inferred patterns of evolution in the trochacean developmental plan are consistent with derivation of caenogastropod developmental timing from a less derived ancestor.

The conclusion that trochaceans are phylogenetically constrained to lecithotrophy and short planktic lives (HESLINGA, 1981) is an extension of the myth that archaeogastropods are rather poorly designed and an evolutionary dead end (HICKMAN, 1988). Adherence to the myth obscures a range of variation in the timing of key developmental events that exceeds the range in caenogastropods, which have achieved flexibility primarily by prolonging settlement (*i.e.*, extending the length of the "delay period" of SCHELTEMA [1967] or "competent period" of HADFIELD [1978]). Underestimation of the variation in trochacean development is also in part a consequence of the schemes most commonly used to classify marine invertebrate development.

DEVELOPMENTAL MODES

The Position of Trochaceans in Classifications of Development

There are many alternative classifications of developmental modes (alternatively referred to as reproductive or developmental types or strategies) in marine invertebrates (see MILEIKOVSKY, 1971; JABLONSKI & LUTZ, 1983). The two dichotomous schemes that are most commonly used both underestimate the amount of variation in trochacean development.

The first classification emphasizes feeding and, in par-

ticular, the dichotomy between larvae that feed in the plankton (the planktotrophs of THORSON, 1950) and those that do not (the lecithotrophs of THORSON, 1950, or nonplanktotrophs of SHUTO, 1974; STRATHMANN, 1978; JABLONSKI & LUTZ, 1980, 1983). In this classification, all trochaceans fall out as nonplanktotrophs. The classification does not distinguish between forms that spend time in the plankton and those that do not; nor does it distinguish between forms that are encased in jelly, encapsulated, or free-living on the bottom or between forms that feed or do not feed on the bottom.

The planktotroph-nonplanktotroph dichotomy has been preferred by some authors (*e.g.*, JABLONSKI & LUTZ, 1980, 1983; BOUCHET, 1989) because it frequently is recognizable in protoconch morphology. As a general rule, the planktotrophic mode of development is reflected in a multispiral protoconch with a small initial whorl and pointed Protoconch I, while the nonplanktotrophic mode is reflected in a large, paucispiral protoconch lacking a sharply demarcated Protoconch I. The morphological accessibility of this criterion has been especially attractive to paleontologists as a means of inferring the developmental mode of extinct gastropods.

A second dichotomous classification focuses on the presence of pelagic or nonpelagic larval development (*e.g.*, CRISP, 1976; SCHELTEMA, 1977, 1978, 1979). In this classification, the major theoretical interest is in the potential for larval dispersal and gene flow over great distances, and SCHELTEMA (1978) has further subdivided the pelagic category to emphasize the importance of the teleplanic larva, one that has a prolonged (6 months to >1 year) life in the plankton. This scheme does not recognize the various ways in which benthic and pelagic forms of development have been mixed in trochacean development.

The Possibility of Feeding in Pelagic Trochacean Larvae

Feeding has not been observed in any trochacean larva to date, but relatively few species have been examined, and those that have been examined are concentrated in a few trochacean subfamilies. ROBERTSON (1985b) urged rejection of the generalization that all archaeogastropods are lecithotrophic (*e.g.*, STRATHMANN, 1978) or nonplanktotrophic (*e.g.*, JABLONSKI & LUTZ, 1983) until more data are available, and he noted that INO (1952) has reported feeding in the plankton by larvae of *Haliotis discus* Reeve, 1846.

Even if feeding on particulate matter can be documented in the veligers of some trochaceans, morphological specialization of the velum and a substantial increase in velar area would be prerequisite to significant nutrition. Specifically, the absence of velar structures, such as the meta-troch (post-oral ciliary band) and ciliated food groove to carry particles to the mouth, argue against effective suspension feeding.

However, particulate matter is not the only available

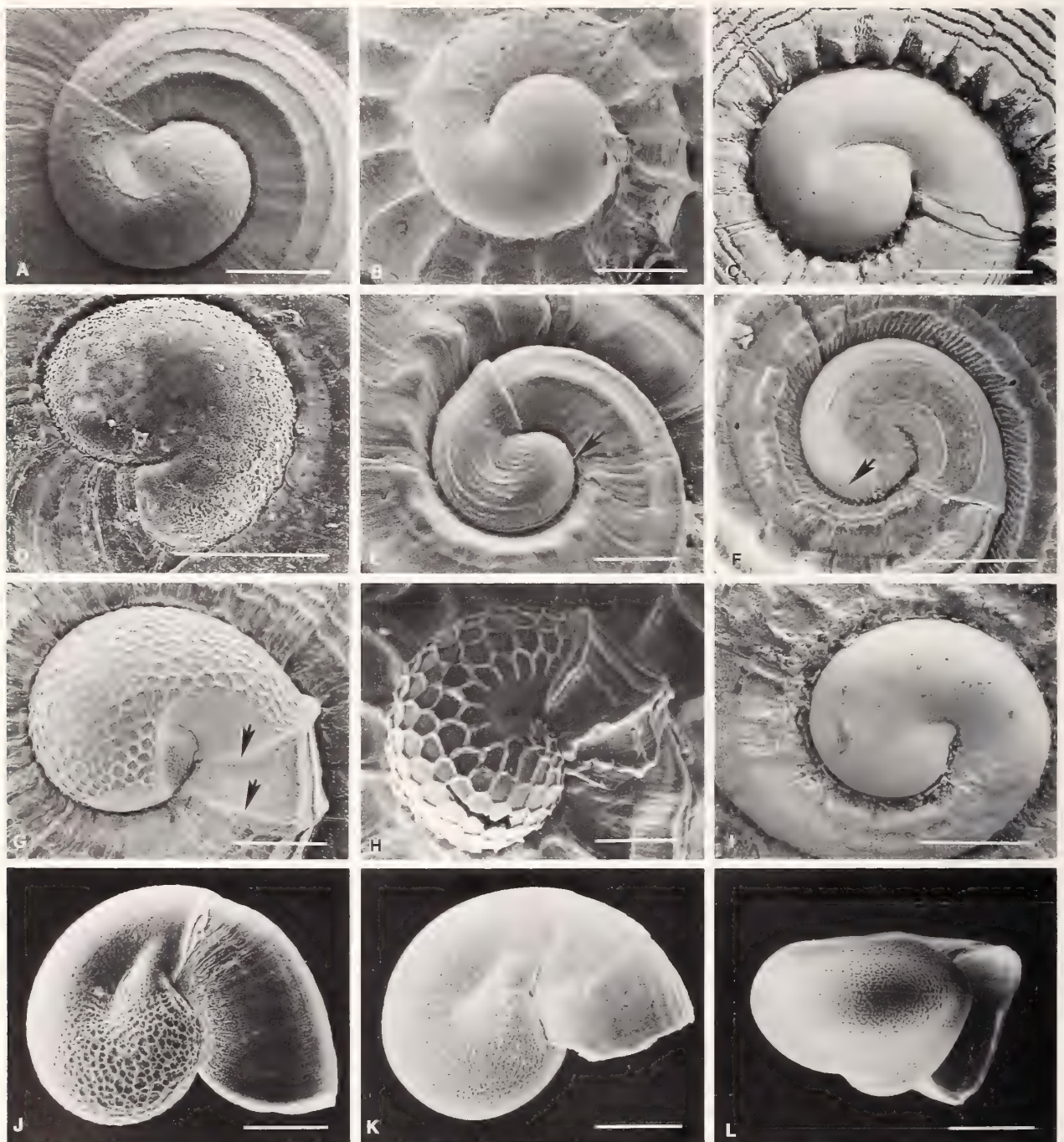


Figure 5

Trochacean protoconchs. A. *Ilanga lirellata* Herbert, 1987 (Trochidae: Solariellinae). Bar = 200 μ m. B. *Calliotropis* sp. (Trochidae: Eucyclinae). Bar = 150 μ m. C. *Lodderena minima* (Tenison Woods, 1878) (Turbinidae: Liotiinae). Bar = 100 μ m. D. *Gabrielona pisinna* Robertson, 1973 (Turbinidae: Gabrieloninae). Bar = 100 μ m. E. *Leptothyra kermadecensis* Marshall, 1979 (Turbinidae: Colloniinae). Bar = 150 μ m, arrow denotes discordant spiral thread. F. *Leptothyra benthicola* Marshall, 1979 (Turbinidae: Colloniinae). Bar = 150 μ m, arrow denotes discordant spiral thread. G. *Herbertina eos* Marshall, 1988 (Trochidae: Thysanodontinae). Bar = 100 μ m, arrows denote time of hatching and time of settlement. H. *Calliostoma (Fautor) consobrina* (Powell, 1958) (Trochidae: Calliostomatinae). Bar = 100 μ m. I. *Crosseola concinna* (Angas, 1867) ("Skeneidae"). Bar = 100 μ m. J. *Lirularia succincta* (Carpenter, 1864) (Trochidae: Lirulariinae), apical view of the mechanically deformed hyperstrophic larval shell and orthos-

source of nutrition to a pelagic larva. JAECKLE & MANAHAN (1989b) have reported uptake of dissolved organic matter (DOM) by pelagic larvae of *Haliotis rufescens* Swainson, 1822, and have shown that the costs of development in this species cannot be met by the energy supply present in the egg (JAECKLE & MANAHAN, 1989a). Uptake of DOM could play a significant role not only in paying developmental costs, but also in meeting metabolic needs if settlement and metamorphosis are delayed.

The Possibility of Feeding in Benthic Trochacean Larvae

When larvae are classified according to a planktotrophic-lecithotrophic dichotomy (e.g., SHUTO, 1974; STRATHMANN, 1978), it is possible to overlook the potential for a nonfeeding planktic larva to begin feeding on the bottom between settlement and metamorphosis. There is no explicit documentation of feeding in this state by trochaceans, but demersal veligers that spend time near or on the bottom, alternately swimming feebly and attempting to crawl, before metamorphosis also have been observed making feeding movements (FRETTER, 1967; UNDERWOOD, 1972b). In larvae of *Gibbula cineraria* in the "swimming-attempted creeping" stage, UNDERWOOD (1972b) noted rapid development of the snout *prior* to shedding of the velum and stated that "the mouth was definitely open and searching movements were made." Whereas there is an abrupt anatomical reorganization associated with the change in feeding mode at metamorphosis in planktotrophic species, adult feeding morphology is able to develop gradually and precociously in the larvae of nonfeeding archaeogastropods without impeding function of the velum (FRETTER, 1969). CROFTS (1937) noted development of the radular diverticulum in *Haliotis* prior to the completion of torsion.

As in the case of unconventional feeding in the plankton (uptake of DOM), benthic feeding by a premetamorphic veliger could be substantial enough to increase its chances of survival (e.g., by prolonging larval life and increasing the probability of encountering the proper substrate for final settlement and/or metamorphosis).

Poecilogony in Trochaceans

HOAGLAND & ROBERTSON (1988) and BOUCHET (1989) reviewed the reports of developmental polymorphism in gastropods and did not find any alleged examples of the

phenomenon in trochaceans. The form of poecilogony that has been of primary interest to malacologists and paleontologists is that of the restricted definition, in which both feeding (multispiral protoconch) and nonfeeding (paucispiral protoconch) larvae are reported either within the same population or within different populations of the same species. Both papers showed that the poecilogony has not been documented conclusively in any marine prosobranch, and that the presence of multispiral and paucispiral protoconchs on shells that are "virtually identical" is most likely an indication that cryptic species are involved.

Developmental polymorphism need not be recorded in the protoconch, however, and the absence of protoconch differences cannot be used to argue against poecilogony in the broader sense of the term. There is no morphological criterion for distinguishing benthic development from pelagic development in the trochacean protoconch (HADFIELD & STRATHMANN, 1990) and insufficient evidence to support or refute the possibility of polymorphism of hatching time that would give rise to both types of development within a single species.

THE TROCHACEAN PROTOCONCH AND ITS INTERPRETATION

Protoconch Morphology

Trochacean protoconch form and sculpture are illustrated in Figure 5A–L. There are relatively few published data on the morphology of the trochacean protoconch, and HICKMAN & MCLEAN (1990) did not use protoconch characters in a systematic revision of the superfamily except to diagnose the subfamily Calliostomatinae, species of which share a distinctive, fine, hexagonal protoconch sculpture (Figures 4, 5H). This same pattern of sculpture occurs on the protoconch of members of the Thysanodontinae (Figure 5G) (MARSHALL, 1988a), and the pattern of character state distributions suggests that thysanodontines are derived from calliostomatines.

The trochacean protoconch shows little variation in form and sculpture relative to the caenogastropod protoconch. This generalization is based on my own survey of representative species of the trochacean subfamilies and tribes and examination of published scanning electron micrographs (RODRIGUEZ BABIO & THIRIOT-QUIÉVREUX, 1974; MARSHALL, 1979, 1988a; BANDEL, 1975, 1982; DOBBERTEN & ELLMORE, 1986; HERBERT, 1987, 1989; COLMAN & TYLER, 1988; HADFIELD & STRATHMANN, 1990). Pro-

← trophic early teleoconch of newly hatched juvenile. Bar = 100 μ m. K. *Margarites marginatus* Dall, 1919 (Trochidae: Margaritinae), apical view of the mechanically deformed hyperstrophic larval shell and orthostrophic early teleoconch of newly hatched juvenile. Bar = 100 μ m. L. *Margarites marginatus* Dall, 1919 (Trochidae: Margaritinae), showing the manner in which the teleoconch of newly hatched juvenile is growing to cover most of the hyperstrophic (apex down) larval shell. Bar = 100 μ m. Micrograph A provided by D. G. Herbert, micrographs E–H by B. Marshall, and micrographs J–L by M. G. Hadfield and M. F. Strathmann.

toconchs are approximately 1.25 whorls. Size is dependent upon egg size and is more closely correlated with water depth than with taxonomic group. The largest protoconchs occur in species with large yolk reserves. Sculpture ranges from smooth at one extreme to the highly ordered hexagonal network of the calliostomatines, although the most common forms of sculpture are weak spiral threads and disordered or weakly ordered patterns of pitting and granulation. The shape of the large apex is bluntly rounded, and it is partially enveloped by the adult shell, so that it is not possible to locate precisely the position or orientation of an axis of coiling (Figure 5A–L).

BANDEL (1982) grouped sculpture of archaeogastropod protoconchs into 10 general types and also concluded that only one, the net-like pattern of *Calliostoma*, was diagnostic of higher taxa. Many protoconchs are completely smooth (Figure 5C, I) or nearly smooth (Figure 5B). More commonly, however, the surface has fine relief that forms distinctive patterns at higher magnifications. One of the commonest patterns of relief is an irregularly anastomosing network of shell material that has a frothy appearance (Figure 5D, J–L). This surface sometimes looks as if it might be the result of secondary dissolution or etching of the protoconch surface (Figure 5D), but it clearly is a primary feature on the shells of larvae reared in the laboratory (Figure 5J–L).

The most extensive set of protoconch illustrations for a single trochacean subfamily is that of HERBERT (1987), who illustrated 27 solarielline species in three genera. Although there is considerable variation in protoconch size (300–800 μm diameter), the number of whorls (1.25) is relatively constant, as is the presence of 3–6 fine spiral threads that are not continuous with the more numerous spirals that begin abruptly on the juvenile shell. Such spirals are not, however, restricted to this subfamily (Hickman, personal observation). Spiral sculpture ranges from a few discrete spiral elements (Figure 5A, F, K, L) to numerous spirals that may be indistinct, wavy, or discontinuous (Figure 5E).

One of the most distinctive aspects of protoconch sculpture is the manner in which spirals appear to be discordant with coiling of the earliest-formed part of the protoconch (e.g., Figure 5E, F). The irregularity of the sculpture figures in arguments about the way the protoconch forms, and has significant bearing on the arguments discussed below about the relationship between the axis of coiling of the protoconch and that of the adult shell.

Heterostrophy in Trochacean Shell Growth

Heterostrophy is a condition in which the whorls of the protoconch appear to be coiled in the opposite direction from those of the adult shell. Heterostrophy is rare in prosobranchs and is considered by some malacologists to have arisen only once, and that at the caenogastropod grade of organization (e.g., ROBERTSON, 1985a). It is therefore

of considerable interest that HADFIELD & STRATHMANN (1990) have observed and illustrated heterostrophic changes in coiling from dextral hyperstrophic protoconchs to dextral orthostrophic teleoconchs in species of the primitive trochid subfamily Margaritinae and in species of the derived trochid subfamily Lirulariinae. Illustrations of hyperstrophic protoconchs from their paper are reproduced in Figure 5J–L.

There are three important pieces of evidence in the argument for trochacean heterostrophy: (1) the trochacean larval shell is initially bilaterally symmetrical, (2) subsequent coiling (or deformation) of the larval shell produces an asymmetric condition in which the apex (or at least the majority of the shell) is displaced to the left (Figure 5L), while (3) at metamorphosis the direction of coiling changes to displace the shell to the right.

Prior to the work of HADFIELD & STRATHMANN (1990) there were a few unillustrated references to heterostrophy in trochaceans (e.g., DALL, 1889b; MINICHEV, 1971). BANDEL (1975) referred to a "left handed evolute start-off" in the protoconchs of gibbuline and cantharidine trochids. I shall argue below that he was describing a phenomenon that produces the appearance of heterostrophy in the early portion of the protoconch only. However, it does not arise from a change in coiling direction during accretionary growth and does not seem to provide a complete explanation of the coiling pattern illustrated by HADFIELD & STRATHMANN (1990).

There are two difficulties in evaluating the nature and extent of heterostrophy in trochaceans. In the first place, the bulbous trochacean protoconch is the extension of a large, cup-shaped embryonic shell in which it is difficult to identify an apex or an axis of coiling. In the second place, most of the trochacean protoconch is enveloped in postlarval growth by the adult shell. Only a small portion of the protoconch is visible once the postmetamorphic juvenile has begun to secrete shell material. It was only by examining larvae and early juveniles (Figure 5L) that HADFIELD & STRATHMANN (1990) were able to detect heterostrophy.

The discovery of heterostrophy in trochaceans is controversial because it has been considered an evolutionary innovation at a higher grade of prosobranch evolution (e.g., ROBERTSON, 1985a; HASZPRUNAR, 1985). However, it is one thing to show that heterostrophy is present in trochaceans and another to show that all heterostrophic shells are homologous. Changes in the direction of coiling between larval and postmetamorphic development may be much more common than heretofore believed, and they may be independently derived in several lineages. Evidence provided by HADFIELD & STRATHMANN (1990) is not sufficient to resolve whether trochacean heterostrophy is a special case of heterostrophy. Heterostrophy is a general phenomenon that is recognized by its geometric expression (HICKMAN, 1980). It may have more than one developmental explanation. The question of homology will be

resolved only by studies of the developmental process. I suspect that trochacean heterostrophy is related less to a leftward displacement of the larval shell through a change in the direction of accretionary growth than it is to a leftward displacement by asymmetric mechanical deformation of the larval shell prior to its mineralization.

Mechanical Deformation of the Trochacean Protoconch During Larval Development

An intriguing, but overlooked, observation by BANDEL (1975, 1982) is the change in apparent direction of coiling that takes place *within* larval development. Although BANDEL (1975) initially described the pointed tip of the protoconch as sinistral in its coiling ("*linksgewundenen*"), he subsequently (1982) interpreted this coiling form as a result of deformation of a poorly mineralized shell rather than as a change in coiling direction during accretionary growth. Furthermore, it is only the tip that is sinistral in appearance, and BANDEL's (1991) interpretation of the larval shell as a whole is that it is mechanically "pulled into the dextral coil."

The most powerful evidence that the initial coil of the protoconch is formed by mechanical deformation rather than accretionary growth is that the discordant spiral sculpture emerges from what appears to be the side of the initial coil rather than from what appears to be the apex (see arrows on Figure 5E, F). In BANDEL's (1982) interpretation, the purely organic, cup-shaped larval shell is bilaterally symmetrical until mechanical deformation occurs. Asymmetric deformation forces it into a trochispiral shape, with the apex on the right and the umbilicus on the left. If, however, asymmetric deformation displaced the apex to the left, it could provide a whole or partial explanation of the observations of HADFIELD & STRATHMANN (1990).

Mechanical deformation has consequences for ecological interpretation and phylogenetic analysis. The amount of mechanical deformation is less in large yolky eggs (BANDEL, 1982), and is correlated with depth. The bulbous, relatively undeformed apex illustrated in Figure 5B is from 250 m. This feature is potentially useful in paleoecological reconstruction. Mechanical deformation is a shared feature of archaeogastropods (*sensu* HICKMAN, 1988), but its distribution among other primitive prosobranch taxa is yet to be determined. It does not occur in neritimorphs.

A major unresolved question is whether mechanical deformation can provide a complete explanation of heterostrophy or whether subsequent growth of the larval shell is displaced to the right, producing additional leftward displacement of the spire. Resolution of this question requires detailed developmental study of live veligers, with careful observation of the timing and sequence of events that include (1) formation, insertion, and contraction of the larval retractor muscle (or muscles), (2) mechanical deformation of the premineralized shell, (3) the fate of the

larval retractor muscle (or muscles) before and during metamorphosis, (4) the origin and assumption of function of the columellar muscle, (5) mineralization of the larval shell, (6) and the onset of accretionary growth.

Evidence of a pattern of deformation is good. A plausible deformational mechanism is difficult to postulate from either of the conflicting interpretations of larval musculature and of the attachment points of the animal to the shell. CROFTS (1955) reported a single larval retractor muscle inserted on the pre-torsional right (post-torsional left) side of the shell. BANDEL (1982) states that there is a pair of larval retractors and that the (post-torsional) left is resorbed after shell deformation, while the (post-torsional) right becomes the precursor of the columellar muscle. Janice Voltzow (personal communication) notes that the larva is attached at two points, but she observes a difference in the nature of the attachment. The attachment on the post-torsional left side is clearly muscular (the single larval retractor of CROFTS [1955] and the (post-torsional) left larval retractor of BANDEL [1982]), but the attachment on the post-torsional right side appears to be connective tissue rather than muscle. In this interpretation, the single left larval retractor is resorbed at metamorphosis and the columellar muscle arises from the post-torsional right mesodermal band.

Ecologic, Biogeographic, and Macroevolutionary Inferences

There is considerable debate over the kinds of interpretations that can be made from the protoconchs of marine prosobranchs. Long before the advent of scanning electron microscopy, it had been suggested that the protoconch was useful in taxonomic distinctions (*e.g.*, POWELL, 1942) and also could be used to infer developmental modes (*e.g.*, THORSON, 1950).

The generalization that species with veligers that feed in the plankton have protoconchs with (1) a small Protoconch I (reflecting small egg size), (2) one or more whorls of Protoconch II (= multispiral), and (3) a morphological distinction between Protoconch I and Protoconch II, is not strongly disputed. Likewise, the generalization that species with nonfeeding larvae have protoconchs with (1) a large initial whorl (reflecting large egg size), (2) few post-nuclear whorls, and (3) lack of a prominent morphological discontinuity has not been questioned.

The interpretations that have been made from these generalizations have fared less well. The three major categories of interpretation have involved (1) the geographic ranges of taxa (as a reflection of dispersal potential), (2) the geologic longevity of taxa, and (3) the rates of speciation and extinction of taxa (see JABLONSKI & LUTZ, 1983, and references therein). Some predictions, such as the ability of larvae with multispiral protoconchs to achieve broad geographic ranges in a single generation (SCHELTEMA, 1977, 1978, 1979) have strong empirical support. Other

predictions, such as species with multispiral protoconchs having broader geographic ranges and longer stratigraphic ranges, are supported less strongly by the correlative observations originally provided by POWELL (1942) and SHUTO (1974), and the subsequent, more refined correlative analyses of HANSEN (1978, 1980) and JABLONSKI (1986).

Anomalies in JABLONSKI's (1986) Cretaceous data set (nonplanktotrophic species with geographic and stratigraphic ranges exceeding those of planktotrophs) have been noted by HADFIELD & STRATHMANN (1990). There is certainly no theoretical reason why a species that totally lacks planktic development cannot achieve a broad distributional range exclusively through the cumulative effects of adult movements over long periods of time.

Any prediction that trochaceans (as taxa with paucispiral protoconchs) will have restricted geographic and stratigraphic ranges and high rates of speciation and extinction is suspect in terms of the developmental variability discussed herein. By focusing on the lack of larval feeding, it lumps taxa with attached benthic development, demersal benthic development, nonfeeding pelagic development, and several forms of mixed pelagic and non-pelagic development. The lumping of these categories involves unwarranted assumptions that seriously underestimate (1) passive dispersal of floating, unattached eggs and embryos, (2) the length of time that nonfeeding larvae can spend in the water column, (3) the extent to which nonfeeding larvae can delay settlement and/or metamorphosis, and (4) the access that nonfeeding pelagic larvae and demersal larvae may have to fast-moving currents (HADFIELD & STRATHMANN, 1990).

CONCLUSIONS

A recurring theme of this paper is the diversity and variability in trochacean reproduction and development that emerges only when comparisons are made in a systematic framework, and only when the traditional expectations of primitive, canalized simplicity are suspended. Most of the published data have been generated outside of a comparative or systematic framework as studies of single species, with a bias toward common intertidal species in the vicinity of marine laboratories.

There are major gaps in comparative systematic data for the families Skeneidae (no data) and Turbinidae (data for only two of the nine subfamilies). In the Trochidae, data are concentrated in taxa in the three tribes of the subfamily Trochinae and the subfamily Calliostomatinae. Although data have been published for species representing four additional trochid higher taxa, there are 12 remaining higher trochid taxa for which there are no comparative data.

Much of the evolutionary novelty in trochacean evolution is based on modifications of the epipodium, and it would be appropriate to look more carefully for dimorphism in the morphology and behavior of anterior epi-

podial structures (especially the right neck lobe). Although previous reports of a trochacean penis have failed to document the implied function of insertion and internal fertilization, the possibility that such structures enhance sperm transfer bears closer scrutiny.

Broadcast spawning and the spawning of benthic egg masses are well-established modes of egg release in trochaceans, leading to planktic larval development on one hand and benthic larval development on the other. We know less about taxa that brood: the variety of sites where brooding occurs and the number of times brooding has arisen in trochacean evolutionary history. Least well understood are the taxa that spawn discrete strings of eggs: the significance of the alternative patterns of spawning unattached strings that disaggregate in the water column soon after spawning, unattached strings that remain intact and sink to the bottom, and strings that are loosely tacked to the substrate. Do eggs benefit from remaining together in the water column, and for how long? Can sinking (after fertilization but before hatching) provide an additional benefit? Is the loose attachment of egg strings an evolutionary step in the direction of benthic development and loss of a planktic stage, or is there an advantage to late hatching and a brief sojourn in the plankton? Mixed benthic and planktic development has been modeled as a discrete adaptive strategy (PECHENIK, 1979; STRATHMANN, 1985). However, the different ways trochaceans combine larval development in the water column and on the bottom confound the notion of a single mixed strategy, and their ultimate evolutionary significance may lie principally in the range of developmental variability they encompass.

Modeling of the mechanics of fluid movements on different spatial scales and of the behavior of particles as a function of their properties is a relatively new field (DENNY, 1988), and experimental studies of the fluid mechanics of broadcast spawning (THOMAS, 1992) show that gamete properties can have important functional consequences. Trochacean gametes and larvae comprise a variable system in which experimental tests might be especially fruitful.

The questions of heterostrophy and mechanical deformation of the trochacean protoconch are especially important to paleontologists because the protoconch is one of the few keys to inferring development in extinct taxa. Interpretation of these phenomena requires additional direct observation of events in larval development. Trochacean protoconchs are not reliable as sources of information about where development takes place (in the water column or on the bottom) or the length of time between fertilization and metamorphosis. They can, however, be read more carefully for information about events that have occurred during larval development.

In summary, it is the unique features of trochacean reproduction and development that seem to provide the most productive avenues for future research. Problems inviting special attention include: (1) the composition, properties, and function of the primary and secondary egg jellies that are characteristic of trochacean eggs; (2) the compar-

ative structure and functional contributions of female palial glands and elaborations (urogenital papillae) in trochacean spawning and reproduction; (3) the effects of different spawning modes on fertilization success and larval dispersal; (4) the possibility that trochacean epipodial structures function in sperm transfer and that internal fertilization may occur; (5) the possibility of unconventional nutrition (uptake of dissolved organic matter) in planktic trochacean larvae; (6) the possibility of feeding in benthic trochacean larvae between settlement and metamorphosis; (7) the nature, extent, and evolutionary significance of the apparent heterostrophy in many trochacean protoconchs; and (8) the nature and significance of the widespread apparent mechanical deformation of the tip of the trochacean protoconch during larval development.

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Systematic Review of the Family Choristellidae (Archaeogastropoda: Lepetellacea) with Descriptions of New Species

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Abstract. The known species in the family Choristellidae Bouchet & Warén, 1979 (= Choristidae of authors) are revised. All occur in continental shelf to abyssal depths and live in spent egg cases of sharks and rays, upon which they feed. The family is assigned to the Lepetellacea by Haszprunar on anatomical characters (1988a, b, c, 1992). Two genera with divergent shell form are recognized: the naticiform *Choristella* Bush, 1897, and the discoidal *Bichoristes*, gen. nov. The radula is unique to the family; shell characters are also diagnostic—extremely thin shell, deep suture (except in *Bichoristes*), complete peristome, sharp umbilical carination, small size, smooth protoconch with bulbous tip, and compressed earliest teleoconch. Previously described species of *Choristella* are *C. tenera* (Verrill, 1882) and *C. leptalea* Bush, 1897, both from the northwestern Atlantic, and *C. vitrea* (Kuroda & Habe, 1971) from Japan. New species proposed here are *C. marshalli* from New Zealand, *C. nofronii* from the Mediterranean, *C. ponderi* from eastern Australia, and *C. hickmanae* from Oregon. The monotypic new genus *Bichoristes* is based on *B. wareni* from New Caledonia. *Bichoristes* is considered to be derived from *Choristella*.

Species previously but incorrectly assigned to *Choristes* Carpenter are discussed in the appendix. *Choristes elegans* Carpenter, 1872, has already been referred to Naticidae, but is here placed as a synonym of *Amauropsis islandica* (Gmelin, 1791).

INTRODUCTION

The family Choristellidae Bouchet & Warén, 1979, comprises a poorly known group of small, thin-shelled, trochiform or naticiform species living offshore at continental shelf to abyssal depths. Living specimens have been collected only within the spent egg capsules of sharks and skates, upon which they feed. Shells are paper-thin and easily crushed.

The Choristellidae are better known in literature prior to 1979 as the Choristidae Verrill, 1882, the family name having been intended for a species for which some unusual details of the radula, jaw, and external anatomy were originally described. The type species of *Choristes*, however, is a fossil species that later proved to be a member of the Naticidae. BOUCHET & WARÉN (1979) restored the original concept of the Choristidae by substituting the family name Choristellidae, a name based on *Choristella* Bush, 1897, another genus proposed in the family.

Until recently, the systematic position of the family Choristellidae has been a matter of speculation. The radula provides few direct clues, as it is neither rhipidoglossate nor taenioglossate. VERRILL (1882) said nothing about the possible familial affinity of Choristidae, although BUSH (1897) reported that “Professor Verrill placed it among the Tectibranchiata.” THIELE (1929), followed by WENZ (1938) and TAYLOR & SOHL (1962), placed Choristidae in the Rissoacea; KEEN (1971) placed it near Vitrinellidae; ABBOTT (1974:90) stated that “it may be a tectibranch.” GOLIKOV & STAROBOGATOV (1975:212, 220) placed Choristidae in Naticacea (as order Aspidophora) “on the basis of shell characters and the shape of the radular teeth.”

HICKMAN (1983) considered the choristellid radula to be close to that of the cocculiniform limpet *Cocculinella* Thiele, 1909. Further evidence in support of affinity between choristellids and cocculiniform limpets was provided by the anatomical investigations of HASZPRUNAR (1988a, b, c), who placed the family in Lepetellacea, noting that

two of the included families, the Addisoniidae and Choristellidae, "have a common ancestry, as revealed by their shared feeding biology (on empty egg-cases of skarks or skates), gill-type (with skeletal rods and mucous zones), and alimentary tract (complete loss of stomach)" (HASZPRUNAR, 1988a:19). Further details on choristellid anatomy and relationships are given by Haszprunar in the accompanying paper (HASZPRUNAR, 1992).

This review started as an effort to give a name to the new eastern Pacific species cited by HICKMAN (1983), but it soon became apparent that additional new choristellids have recently been collected and have been awaiting attention in other museum collections. Here I update the classification of the family and add one new genus and five new species. Taxa removed from the family are discussed further in the Appendix to this paper.

MATERIALS AND METHODS

This review is hampered by a shortage of well-preserved material in collections. No material of the first and second named members of the family has been collected in recent years, and none of the original material remains wet-preserved, making it difficult to verify the early descriptions of soft parts by examination of original material. It is only the newly collected material of the species described here that has made it possible for HASZPRUNAR (1988a, b, c, 1992) to report on the internal anatomy.

Radulae were extracted after dissolution of tissue in 10% NaOH at room temperature; dry specimens of *Choristella tenera* were first rehydrated in detergent prior to treatment in NaOH. The radular ribbons were washed in distilled water, dried from a drop of water placed on a stub having a thin smear of rubber cement, and coated with gold or gold/palladium for examination with SEM. Jaws were also extracted with room temperature NaOH and examined with SEM. Preserved specimens were critical point dried and examined with SEM.

All depths that were originally cited in fathoms have been changed to meters.

Abbreviations of institutions mentioned in the text: AMS, Australian Museum, Sydney; BMNH, Natural History Museum, London; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Museum National D'Histoire Naturelle, Paris; NMNZ, National Museum of New Zealand, Wellington; NZOI, New Zealand Oceanographic Institute, Wellington; USNM, National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Order ARCHAEOGASTROPODA Thiele, 1925

Suborder COCCULINIFORMIA Haszprunar, 1987

Superfamily LEPETELLACEA Dall, 1892

Although a monofamilial superfamily has been proposed for the Choristellidae (Choristiacea Kuroda & Habe, 1971,

emended to Choristelliacea by HICKMAN, 1983), HASZPRUNAR (1988c) united the families Lepetellidae, Bathyphytophilidae, Pyropeltidae, Pseudococculinidae, Osteopeltidae, Cocculinellidae, Addisoniidae, and Choristellidae in the Lepetellacea, on the basis of sharing compact shell muscles, two kidneys, separated gonad with simple gonoducts, and statocysts with several statocones.

Except for the Choristellidae, the lepetellaceans are hermaphroditic limpets. The family Choristellidae is the only member having a coiled shell and the only member that is gonochoristic.

Family CHORISTELLIDAE Bouchet & Warén, 1979

CHORISTIDAE of authors (see below): VERRILL, 1882:540; THIELE, 1929:179; CLARKE, 1961:359; KEEN, 1971:388; ABBOTT, 1974:90; BOSS, 1982:1010.
CHORISTELLIDAE BOUCHET & WARÉN, 1979:225; HICKMAN, 1983:86; HASZPRUNAR, 1988c:66.

Included genera: *Choristella* Bush, 1897, and *Bichoristes* McLean, gen. nov. *Choristella* species are defined by differences in shell proportions, opercular coiling, and external anatomy, although knowledge of external anatomy remains incomplete. *Bichoristes* is monotypic and based on a single specimen for which the shell, radula, operculum, and jaw are known. The description of external anatomy in the diagnosis that follows is based on that of *Choristella*.

Diagnosis: Shell small (maximum dimension not exceeding about 10 mm), extremely thin, periostracum thin; whorls 3 to 3.5, rounded or carinate (carinate only in *Bichoristes*); suture deeply channeled (except in *Bichoristes*); spire height low to moderate; peristome complete, area of contact minimal; final lip slightly flared; umbilicus narrow to wide; umbilical wall with sharp descending carina. Protoconch diameter 250–300 μ m, tip bulbous, surface smooth. Operculum of 3–10 whorls, multispiral to paucispiral.

Jaw of two prominent, dark brown, finely reticulate plates, fused dorsally, laterally bowed to produce oval mouth opening with jagged edge.

Radula. Rachidian tooth triangular, with short base and bluntly pointed overhanging cusp. First lateral tooth with quadrangular shaft, singly cusped in *Choristella*, bicuspid in *Bichoristes*. Second lateral tooth with long shaft, bicuspid in *Choristella*, unicuspid in *Bichoristes*. Third lateral tooth with long shaft and pointed cusp. Fourth lateral tooth similar, except reduced and fused to third in *Bichoristes*. Fifth lateral tooth vestigial.

Remarks: MARINCOVICH (1975, 1977) correctly placed *Choristes* Carpenter in Dawson, 1872, in the Naticidae (see further notes on *Choristes elegans* under excluded species), which left the living species of *Choristes*, of authors, in limbo. Without citing Marinovich, BOUCHET & WARÉN (1979) proposed Choristellidae in a brief note. They wrote: "We want to use this occasion to point out that the genus *Choristes* Carpenter MS, Dawson, 1872 is a naticid. An

examination of the types of *Choristella leptalea* Bush, 1897 (type species of *Choristella*) and *C. tenera* Bush, 1897 [evidently a lapsus for *C. brychia* Bush, 1897] has proved that they are synonyms of *Choristes elegans* var. *tenera* Verrill, 1882. Verrill's name therefore has to be used for the type species. Another consequence is that the name Choristidae has to be changed to Choristellidae."

BOSS (1982) missed the proposal of Choristellidae and followed MARINCOVICH (1977) in leaving all species described under *Choristes* within the Naticidae.

Diagnostic shell characters for Choristellidae are the extremely thin shell, smooth protoconch with a bulbous tip, maximum of 3.5 teleoconch whorls, the complete peristome, and the sharp carination that descends within the umbilicus. Additionally, *Choristella* has a deeply channeled suture. Surprisingly, the descending umbilical carination has not previously been noticed, although it provides a consistent shell character for the family.

The overall aspect of the radula is similar in the two genera, but differs in having the first lateral bicuspid in *Bichoristes* and the second lateral bicuspid in *Choristella*. Shared features are that the lateral teeth are robust and slope away from the rachidian, and that the shafts of the rachidian and first lateral are relatively short, whereas those of the second, third, and fourth laterals are longer and articulate together, and the fifth lateral is vestigial.

The choristellid radula cannot be confused with that of any other family. Despite a statement (HICKMAN, 1983: 86) about radular affinity with the Cocculinellidae ("same basic pattern"), the resemblance is superficial. The cocculinellid radula, as illustrated by MARSHALL (1983), has the rachidian flanked by a pair of small teeth, followed by a series of stout interlocking teeth of similar morphology with serrate outer edges. Marshall considered the latter to be marginal teeth and the lateral teeth to be represented by the small inner pair. The choristellid radula differs in having the rachidian flanked by massive teeth and none of the succeeding teeth in the row are similar. The bicuspid second lateral tooth of *Choristella* and the bicuspid first lateral tooth of *Bichoristes* are evidently fused from the primitive condition for the family, which is not represented in a living genus. The teeth of both families are probably homologous, but I am more inclined to regard the teeth of each family as lateral teeth than as marginals for two reasons: I know of no other examples of massive lateral teeth and the paired teeth of the choristellid radula could hardly be considered marginals because they have laterally extended shafts, as well as exhibiting partial fusion.

The choristellid protoconch has a bulbous tip, similar to that of the Cocculinidae (see MARSHALL, 1986:fig. 5D), but unlike the compressed and laterally pinched tip of the cocculinellid protoconch (MARSHALL, 1983:fig. 1I) or the pseudococculinid protoconch (MARSHALL, 1986:fig. 9H). Close affinity with either family is therefore not supported on evidence from the protoconch. Unfortunately, the adisoniid protoconch remains unknown (MCLEAN, 1985) and it is not yet possible to confirm with protoconch evi-

dence the affinity of the two families as advocated by HASZPRUNAR (1992) on anatomical evidence.

Genus *Choristella* Bush, 1897

Choristes Carpenter, of VERRILL, 1882:540; DALL, 1908:328; THIELE, 1929:179; CLARKE, 1961:359; KEEN, 1971:388; ABBOTT, 1974:90. Not *Choristes* Carpenter in Dawson, 1872 [Naticidae].

Choristella BUSH, 1897:138; THIELE, 1929:179; BOUCHET & WARÉN, 1979:225; HICKMAN, 1983:86.

Type species (original designation): *Choristella leptalea* Bush, 1897.

Diagnosis: Shell small (maximum dimension about 10 mm), extremely thin (maximum thickness of broken edge 0.05 mm), easily damaged; periostracum thin; whorls 3 to 3.5, rounded; suture deeply channeled, spire height low to moderately high. Peristome complete, contact with previous whorl limited to narrow band; final lip flared but not thickened, reflected near base of columella. Umbilicus narrow to broad, umbilical wall with sharp descending carina that terminates on reflected region of lip at base of columella. Protoconch diameter 250 μ m, surface smooth; tip bulbous. Outer edge of first quarter turn of teleoconch compressed, not forming regular curve. Operculum thin, up to 5 whorls, multispiral or with final whorl enlarged to give paucispiral effect.

External anatomy. Snout prominent, eyes lacking, cephalic and epipodial tentacles lacking micropapillae. One to two suboptic tentacles short, posterior to right cephalic tentacle. Gill pectinibranch, leaflets numerous. Sexes separate; male using right cephalic tentacle as copulatory organ; open seminal groove on right tentacle.

Jaw. As described for family.

Radula. Rachidian tooth relatively small, with triangular shaft and small overhanging cusp; base of shaft broadly emerging from ribbon. First lateral tooth massive, shaft quadrangular, overhanging cusp large, triangular, with bluntly pointed tip; base of shaft articulating with tooth below, base of shaft buttressed on inner and outer edges; second lateral tooth separated from third by open channel. Second lateral tooth largest in row, with two large cusps, the innermost with triangular cusp matching that of second lateral, the outermost cusp having a more obtuse angle; position of both cusps descending away from rachidian; base with projecting ridge above excavation that accommodates tooth below. Third lateral tooth with long shaft and thick, rounded cusp that projects over the outer cusp of second lateral tooth; base buttressed on inner side by narrow ridge. Fourth lateral tooth with longest shaft and small, beaklike cusp, base buttressed on inner side by projecting ridge. Fifth lateral tooth vestigial, closely appressed to base of fourth lateral tooth.

Remarks: *Choristella* species may be recognized on shell characters alone (thin shell, channeled suture, complete peristome, compression of early teleoconch, and descending umbilical carination). The descending umbilical carination

may be shared with some skeneiform genera, including *Trenchia* Knudsen, 1964, as discussed here under rejected species. On shell characters, *Choristella* may be distinguished from such genera in having a much more deeply channeled suture and by the compression of the early teleoconch (for the latter see especially Figure 22).

The radulae of all species examined are closely similar. Some differences that may be apparent in the illustrations for each species can be attributed to wear, rather than interspecific differences. The most useful radular characters for interspecific discrimination are the morphology and relative size of the rachidian tooth.

The bulbous tip of the protoconch is treated under the family heading. In some species the protoconch remains unknown; in all the available specimens of such species it is replaced by a calcareous plug, representing an internal mold of the original protoconch (see Figure 11).

In proposing *Choristella*, BUSH (1897) emphasized a radular difference from *Choristes*. According to Bush, *Choristella leptalea* has 13 teeth in the row, as opposed to 11 teeth in *Choristes elegans* var. *tenera*. Both CLARKE (1961: 359) and BOUCHET & WARÉN (1979) discounted a radular distinction, and attributed the tooth count discrepancy to varying interpretations of the second lateral tooth either as a bicuspidate compound tooth or two separate teeth. I interpret the second tooth as a compound tooth derived by fusion of two separate teeth. BOUCHET & WARÉN (1979: fig. 12) provided a drawing of the radula of *Choristella tenera* that showed the rachidian and five lateral teeth, making a total of 11 teeth in the row. That interpretation of the radula is followed here. Although the radula of *Choristella leptalea* is not available for SEM study, a generic distinction based on radulae is evidently unfounded.

Despite the lack of evidence from the radula, the conclusion that the taxa proposed separately by Verrill and Bush are the same is not supported here. There are other, more important differences, one of which was well figured in the original accounts: the operculum of *Choristella tenera* is shown with three whorls and expands so rapidly that it looks to be paucispiral (see VERRILL, 1882: pl. 58), whereas the operculum of *C. leptalea* is shown as multispiral, with five whorls (BUSH, 1897: fig. 8). There are also differences in shell proportions between the two species: *C. leptalea* is clearly lower-spined than *C. tenera*, and is smaller. Both have the same number of whorls, which suggests that they are based on mature specimens. There are also differences in the external anatomy that can be detected from a careful reading of the original descriptions.

Bush recognized two species and intended to place them in separate genera. I accept that there are two species (contrary to BOUCHET & WARÉN, 1979, who recognized only one), but am unable to support a generic distinction. The other species treated here cannot be placed into two separate groups on characters now available. Unfortunately, the replacement of *Choristes* by *Choristella* changes the type species of the nominate genus to *Choristella leptalea*, a species that remains poorly known.

On the basis of shell proportions there are two groups of species in *Choristella*, a relatively high-spined group and a relatively low-spined group. Opercular characters do not support generic groupings based on shell proportions, however. High-spined species are *C. tenera* (Verrill, 1882), *C. vitrea* (Kuroda & Habe, 1971), *C. marshalli* sp. nov., and *C. nofronii* sp. nov. Low-spined species are *C. leptalea* Bush, 1897, *C. ponderi*, sp. nov., and *C. hickmanae*, sp. nov.

Choristella tenera (Verrill, 1882)

(Figures 1–7)

Choristes elegans var. *tenera* VERRILL, 1882: 541, pl. 58, figs.

27 [shell with operculum], 27a [radula]; VERRILL, 1884:

256, pl. 29, figs. 9, 9a, 9b [shells of 3 juvenile specimens].

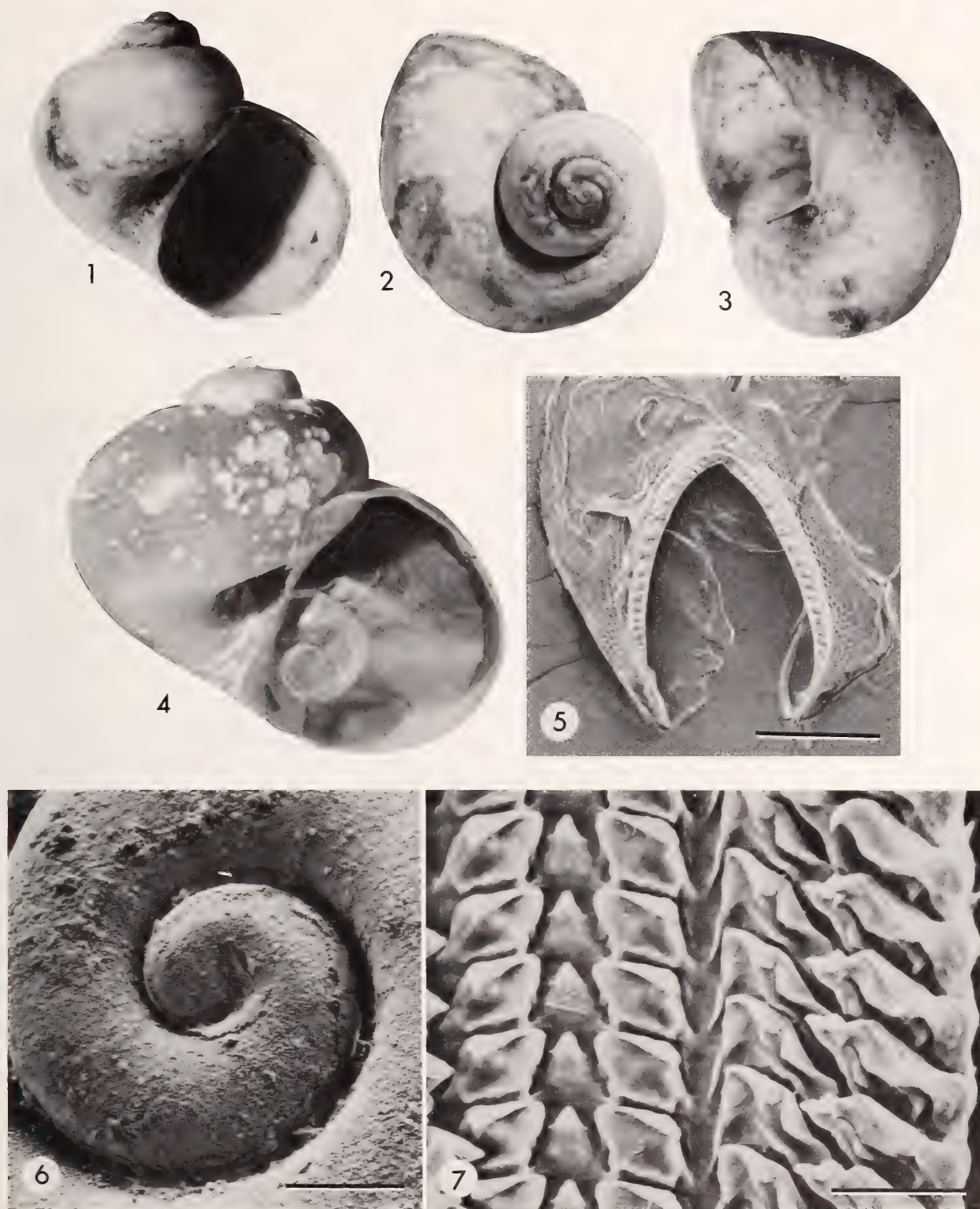
Choristes tenera: CLARKE, 1961: 360; ABBOTT, 1974: 90, fig. 865 [copy figs. of VERRILL, 1882].

Choristella tenera: BOUCHET & WARÉN, 1979: 225, fig. 225 [new drawing of radula, based on paratype, USNM 45151].

Description: Shell (Figures 1–4) large for genus (maximum diameter 10.5 mm), spire height relatively high (height–width ratio of holotype 0.87). Shell wall extremely thin. Surface shiny, brown, periostracum thin, surface finely pitted. Protoconch usually eroded and filled with secondary plug, separated from first teleoconch whorl. Teleoconch whorls 3.5, rounded, smooth; suture deeply impressed. Umbilicus narrow, deep, not obstructed by reflection of inner lip. Spiral sculpture represented by fine striae strongest on base and by single narrow ridge deep within umbilicus; axial sculpture lacking except for fine growth increments. Peristome complete, area of contact with previous whorl minimal. Lip flared at base of columella where buttressed by umbilical ridge. Operculum (Figure 4) pale brown, nucleus slightly excentric, 3 whorls, inner edge growing under outer edge of previous whorl (which raises the outer edge of previous whorls), final whorl expanding to produce paucispiral pattern.

Dimensions. Height 5.4 mm, width 6.2 mm (holotype); height 9.0 mm, width 10.5 mm (largest specimen, USNM 78902).

External anatomy. Because freshly collected, preserved specimens are not available, VERRILL's (1882) original description of the animal is repeated here: "Head large, short, thick, rounded or truncate, with two short, flat, obtuse anterior tentacles, wide apart, but connected together by a transverse fold; posterior tentacles short, thick, conical, smooth; no eyes visible; proboscis [buccal mass] short, thick, retractile; jaws crescent-shaped, strong, black. Verge situated just below the right posterior [error for anterior?] tentacle, small, papilliform, swollen at base; below this and farther back, a larger and thicker papilla with basal swelling; on each side, between the mantle and foot, at about midlength of the foot, a small mammiform papilla; and two small flat cirri, behind and beneath the operculum. Foot broad, ovate, with two tentacle-like pro-



Explanation of Figures 1 to 7

Figures 1–7. *Choristella tenera* (Verrill, 1882). Figures 1–3. Holotype, USNM 45151, off Martha's Vineyard Island, Massachusetts, USA. Height 5.4 mm. Apertural, oblique spire, and umbilical views. Figure 4. Largest specimen, showing operculum in place, USNM 78902, USFC Sta. 2730, off Cape Hatteras, North Carolina. Height 9.0 mm. Figure 5. SEM view of jaw, USNM 78902. Scale bar = 200 μ m. Figure 6. Protoconch, USNM 45253. Scale bar = 100 μ m. Figure 7. SEM view of radula, USNM 78902. Scale bar = 40 μ m.

cesses in front. Gill large, consisting of numerous thin lamellae, attached to the inner surface of the mantle, over the left side of the neck, and extending obliquely across and over the neck to the right side."

Jaw (Figure 5). Typical for family.

Radula (Figure 7). Characteristic for family. Rachidian tooth stout, relatively broad, tip apparently not overhung in present preparation.

Type locality: Off Martha's Vineyard Island, Massachusetts, USFC Sta. 1031, 466 m, "taken from the interior of an old egg-case of a skate (*Raia*, sp.)."

Type material: Holotype, USNM 45151, USFC Sta. 1031, collected in 1881, shell intact, body dried. Eight paratypes in similar condition, USNM 859486. USNM 508720, USFC Sta. 1031, 1 paratype same station as type lot. The shell surface of the type lot is dull from prior preservation in alcohol, although other specimens have a shiny surface.

Referred material: 7 USNM lots, all dry, most with dried bodies: USNM 45252, USFC Sta. 1096, 580 m off Martha's Vineyard, 4 broken shells, one loose body attached to operculum. USNM 45253, USFC Sta. 1124, off Martha's Vineyard, 2 large and numerous small shells. USNM 45254, USFC Sta. 1154, 353 m off Martha's Vineyard, 1 shell, operculum in place. USNM 45255, USFC Sta. 2234, off Martha's Vineyard, 1 shell, operculum in place. USNM 40309, USFC Sta. 2262, off Nantucket Shoals, 3 shells, opercula in place. USNM 78902, USFC Sta. 2730, off Cape Hatteras, North Carolina, 1 large and several small shells, all with opercula in place. USNM 78901, USFC Sta. 2731, off Cape Hatteras, North Carolina, 4 small shells, 2 with dried bodies.

Remarks: All specimens have the sharp, steeply descending umbilical carination, a diagnostic character that was missed by VERRILL (1882) in the original description and not subsequently noticed. Verrill reported that large specimens have 4 to 5 whorls, but this is clearly in error, as the largest specimens do not exceed 3.5 whorls. Verrill compared it to a small specimen of *Choristes elegans* Carpenter, which he had received from Dawson (VERRILL, 1882:542, pl. 58, fig. 28), considering it "a thin and delicate variety of the ancient type."

Verrill's description of the external anatomy noted a "verge" [penis] posterior to the right cephalic tentacle, but this is here regarded as a suboptic tentacle.

Choristella marshalli McLean, sp. nov.

(Figures 8–15)

Description: Shell (Figures 8–10) large for genus (maximum diameter 8.8 mm), spire height relatively high (height–width ratio of holotype 0.90). Shell wall extremely thin, maximum thickness of broken lip 0.05 mm. Surface shiny, light brown; periostracum thin, surface finely pitted. Protoconch usually etched away and filled with secondary

plug, separated from first teleoconch whorl. Teleoconch whorls 3.3, rounded, smooth; suture deeply impressed. Umbilicus narrow, deep, not obstructed by reflection of inner lip. Spiral sculpture represented by fine striae and by single narrow ridge deep within umbilicus; axial sculpture lacking except for fine growth increments. Peristome complete, area of contact with previous whorl minimal. Lip flared at base of columella where buttressed by umbilical ridge. Operculum (Figure 12) pale brown, nucleus slightly excentric, final 3 whorls evenly expanding.

Dimensions. Height 7.9 mm, width 8.8 mm (holotype).

External anatomy (Figure 14). Right cephalic tentacle of male with open groove.

Jaw (Figure 13). Typical for family.

Radula (Figure 15). The radula closely approximates that given for the familial description. The shaft of the rachidian is well marked and there is a small overhanging tip. The outermost tooth in the row is unusually well developed.

Type locality: SE of Banks Peninsula (44°55.4'S, 174°04.9'E), New Zealand, 1097–1116 m, in empty skate egg case.

Type material: 26 specimens—11 intact shells, 15 specimens with broken shells and bodies preserved in alcohol—from type locality, R/V *James Cook*, Sta. J10/37/84, 15 June 1984. The visceral mass has disintegrated in the preserved specimens, which were initially preserved by freezing. Holotype NMNZ M.109053 and 23 paratypes NMNZ M.75210; 1 paratype LACM 2247; 1 paratype AMS.

Referred material: NZOI Sta. I32 off Cape Brett, New Zealand (35°11.7'S, 174°49.8'E), 376–450 m, R/V *Tangaroa*, 7 May 1975, 2 dried, damaged specimens and 1 small preserved body. NZOI Sta. P292, Tasman Basin (40°42.8'S, 167°56.0'E), 1029 m, 4 preserved specimens, shells broken. NMNZ M.89950, NE of Chatham Island, New Zealand (42°52.3'S, 175°37.3'E), 1032 m in elasmobranch egg case, F/V *Akagi Maru*, 9 June 1987, about 15 decalcified or broken-shelled juveniles in alcohol plus about 12 small specimens with dried bodies (SEM of early whorls, Figure 11).

Remarks: This species is characterized by its relatively large size and high spire. It resembles *Choristella tenera* in its size and proportions, but has a less prominent periostracum. As in *C. tenera*, the protoconch of most specimens is etched away, leaving only a plug that is well separated from the first teleoconch whorl (Figure 11). The operculum (Figure 12) is like that of *C. tenera*, although it has more numerous whorls and the final whorl is not so rapidly expanding.

The open seminal groove on the right cephalic tentacle is visible in the critical point dried specimen examined with SEM (Figure 14).

HICKS (1986) reported that skate egg cases containing



Explanation of Figures 8 to 15

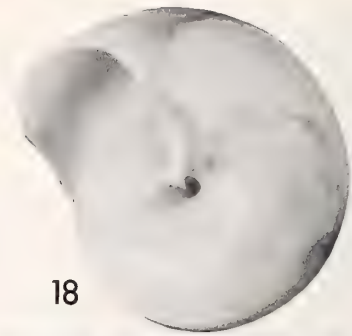
Figures 8–15. *Choristella marshalli* McLean, sp. nov. Figures 8–10. Holotype, NMNZ 75210, SE of Banks Peninsula, New Zealand. Height 7.9 mm. Apertural, oblique lateral, and umbilical views. Figure 11. Early Whorls, showing plug filling protoconch, NMNZ M.89950, NE of Chatham Islands, New Zealand. Scale bar = 200 μ m. Figure 12. SEM view of operculum, NMNZ 75210, paratype. Scale bar = 1 mm. Figure 13. SEM view of jaw, NMNZ 75210, paratype. Scale bar = 200 μ m. Figure 14. SEM view of critical point dried paratype, anterior view of body attached to operculum, showing groove on right cephalic tentacle (arrow), NMNZ 75210, paratype. Scale bar = 1 mm. Figure 15. SEM view of radula, NMNZ 75210, paratype. Scale bar = 40 μ m.



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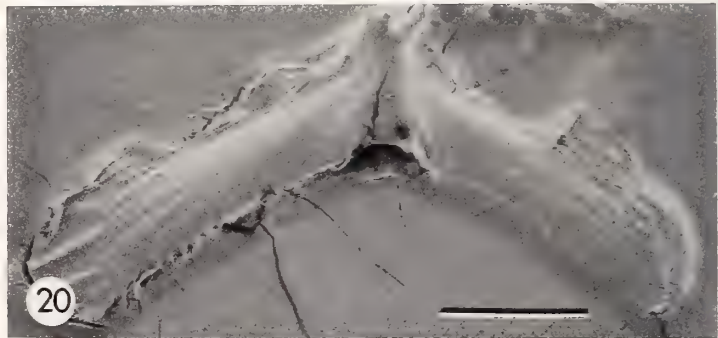
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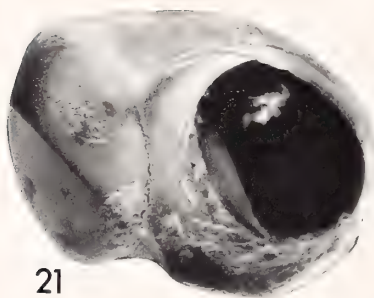
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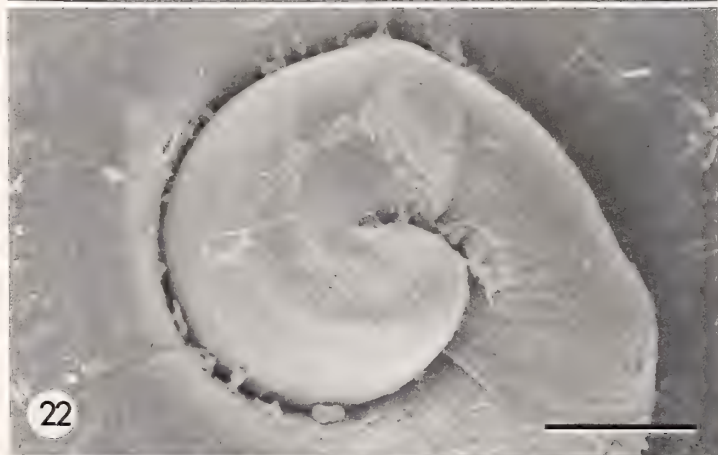
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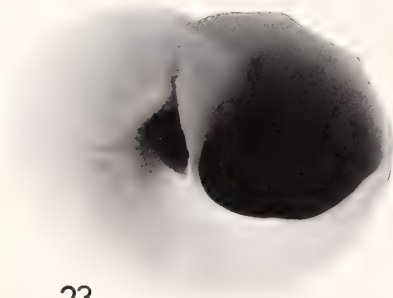
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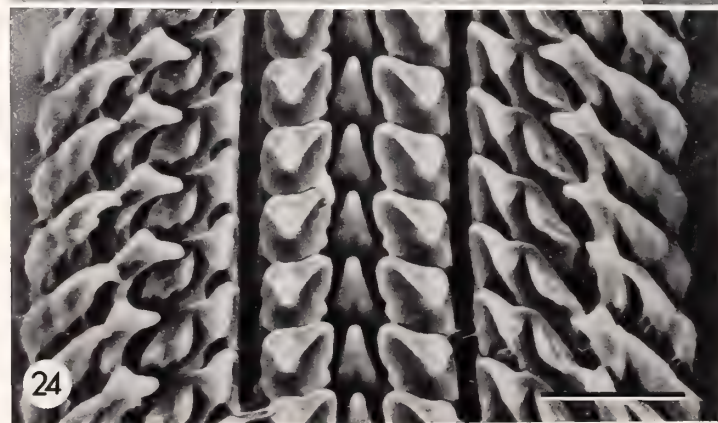
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Choristella species (cited here as the type material of *C. marshalli*) also yielded type material of the harpacticoid copepod *Paramphiascopsis waihonu* Hicks, 1986. Harpacticoids have been noted to feed on microbiota associated with fecal pellets (HICKS, 1986).

Etymology: The name honors Bruce A. Marshall of the National Museum of New Zealand, Wellington.

Choristella vitrea (Kuroda & Habe, 1971)

Choristes vitreus Kuroda & Habe in KURODA, HABA & OYAMA, 1971:62, pl. 107, fig. 11.

Description (copied from Kuroda & Habe): "Shell rather small, thin, translucently white, turbinate in shape. Spire conical and with 5 whorls, rather rapidly increasing their width to the body whorl, well inflated and separated by the deeply impressed sutures. Surface smooth and polished and covered by a thin periostracum and sculptured by the very faint spiral threads and growth lines. Body whorl large and well rounded at the periphery and the base. Aperture wide and semicircular. Outer margin well rounded, thin and slightly expanded. Innermargin [sic] deposited the thin callus on the parietal wall and rather straight [sic]. Columellar margins reflexed and dilated over the widely and deeply perforated umbilicus. Operculum thin, corneous, pale yellowish brown and paucispiral."

Dimensions. Height 10.7 mm, diameter 9.5 mm (holotype); height 12.2 mm, diameter 9.4 mm (paratype).

Type locality: Sagami Bay, Japan, "parasitic on the egg capsules of shark," depth not indicated.

Type material: Holotype and paratype, presumably in Imperial Household Collection, Japan. No other specimens are known.

Remarks: Although the original material has not been examined and the radula has not been described, the description of this species is compatible with that of the high-spired species group of *Choristella*. The shell is comparable to *C. tenera* in size, thinness of shell, and opercular morphology, and to *C. nofronii* in having the height of the shell exceed the breadth. The operculum was said to be paucispiral. The height-width ratio of the holotype is 1.3, compared to 1.13 for *C. nofronii*.

Choristella nofronii McLean, sp. nov.

(Figures 16–24)

Cithna naticiformis Jeffreys, 1883, of GUBBIOLI & NOFRONI, 1986:204 [figures not numbered, size not indicated], *non Cithna naticiformis* Jeffreys, 1883

Description: Shell (Figures 16–18) medium size for genus (maximum height 6.1 mm), spire height relatively high (height-width ratio of holotype 1.13). Shell wall extremely thin, maximum thickness of broken lip 0.05 mm. Surface shiny, yellowish white, periostracum thin. Protoconch (Figures 21, 22) diameter 250 μ m, surface smooth. Teleoconch whorls 2.7 rounded, smooth; suture deeply impressed. Umbilicus narrow, deep, partially obstructed by reflection of inner lip. Spiral sculpture of faint striae and single narrow ridge deep within umbilicus, terminating at columellar flare. Base of mature shell rounded, that of immature shell with angulation. Axial sculpture of extremely fine growth increments, sharply raised on umbilical slope. Peristome nearly complete. Operculum (Figure 19) pale brown, nucleus slightly excentric, final whorl becoming paucispiral.

Dimensions. Height 6.1 mm, width 5.4 mm (holotype).

Jaw (Figure 20). Typical for genus.

Radula (Figure 24). Typical for the family; the shaft of the rachidian is weakly projecting, the overhanging tip of the rachidian is small but clearly revealed.

Type locality: Alboran Sea, westernmost Mediterranean, west of Cabo de Gata, Spain (extending from 01°30'W and 35°30' to 36°30'N, according to P. Bouchet), 50–100 m.

Type material: Holotype (Figures 16–18) MNHN uncataloged, operculum and radula scanned. Four paratypes MNHN uncataloged (heights 5.2, 3.1, 1.7, 1.2 mm). Two paratypes LACM 2248 (height 3.0 mm, protoconch scanned; height 4.1 mm, lip broken). All specimens from the generalized type locality, obtained by I. Nofroni from local fishermen.

Referred material: AMS C.167316, Al Hoceima, Morocco (35°14'N, 03°56'W), 50–100 m, with *Raja* egg cases, August 1986, F. Gubbioli, 2 dry specimens.

GUBBIOLI & NOFRONI (1986) wrote: "All our findings, dozens of specimens, many live, come from eggs of *Raja*

Explanation of Figures 16 to 24

Figures 16–24. *Choristella nofronii* McLean, sp. nov. Figures 16–18. Holotype, MNHN, Alboran Sea, western Mediterranean. Height 6.1 mm. Apertural, spire, and umbilical views. Figure 19. SEM view of operculum of holotype. Scale bar = 1 mm. Figure 20. SEM view of jaw of holotype (elements separated). Scale bar = 200 μ m. Figure 21. SEM view of larval shell, topotypic material, courtesy A. Warén. The straight diagonal line is an artifact of scanning. Scale bar = 100 μ m. Figure 22. SEM view of protoconch and first teleoconch whorl of paratype, LACM 2248. Scale bar = 100 μ m. Figure 23. SEM, oblique umbilical view of juvenile shell showing basal ridge, topotypic specimen, courtesy A. Warén. Scale bar = 1 mm. Figure 24. SEM view of radula, paratype, LACM 2248. Scale bar = 40 μ m.

cf. *clavata* fished in the quadrilateral Marbella, S. Roque (Spain), Tetuan, Al Hoceima (Morocco) at depths between 50 and 100 m."

Remarks: *Choristella nofronii* is characterized by its relatively small size and high profile. In addition, small shells have a weak mid-basal ridge, a feature not observed in any other species.

GUBBIOLI & NOFRONI (1986) found this species in 5% of 250 of the egg cases they examined and found that three times as many had specimens of the limpet *Addisonia lateralis* (Requien, 1848). Both species were noted in 3% of the examined egg cases.

The choristellid affinity was unknown by GUBBIOLI & NOFRONI (1986), who identified it as "*Cithna*" *naticiformis* Jeffries, 1883. The basal ridge that characterizes small shells (Figure 23) led them to associate the species with Jeffreys' taxon from 1453 m (795 fm) off the Portuguese coast. However, the basal ridge of that species (syntypes, BMNH 85.11.5.1615–1617, Figures 60, 61) is much more pronounced, and there is a concave rather than convex surface between the umbilical and basal ridges. Jeffreys' species is treated further in the Appendix.

GUBBIOLI & NOFRONI (1986) also suggested that "*Cyclostrema*" *valvatoides* Jeffreys, 1883, might also be referable to the present species. I have examined the holotype of that species (BMNH 85.11.5.1593). Choristellid affinity is ruled out because it does not have the umbilical ridge characteristic of the family.

Etymology: The name honors Italo Nofroni, one of the collectors of the original material.

Choristella leptalea Bush, 1897

(Figures 25–29)

Choristella leptalea BUSH, 1897:139, text fig. 8 [operculum], text fig. 9 [shell], pl. 23, figs. 16, 16a [radula].

Choristella brychia BUSH, 1897:139, text fig. 10 [spire view of shell].

Description: Shell (Figures 25–29) small for genus (maximum diameter 4.0 mm), spire height relatively low (height–width ratio of holotype 0.71). Shell wall extremely thin. Shell white, periostracum thin, light brown. Protoconch diameter about 300 μ m. Teleoconch whorls 3.4, rounded, smooth, suture deeply impressed. Umbilicus narrow, deep, not obstructed by reflection of inner lip, inner extent of umbilicus defined by narrow ridge. Spiral sculpture lacking; axial sculpture lacking, except for fine growth increments. Peristome complete, area of contact with previous whorl minimal; lip flared below, broadest at base of columella, where meeting umbilical ridge. Operculum of 4.5 whorls, nucleus slightly excentric, final 3 whorls evenly expanding in multispiral pattern.

Dimensions. Height 2.5 mm, width 3.5 mm (original measurements of holotype); height 3.1 mm, width 4.0 mm (new measurements of holotype of *Choristella brychia*).

External anatomy. BUSH's (1897) description is copied

here: "The animal has a broad emarginate head with one pair of long slender tentacles; with a rather broad, short, tapered, ciliated verge just beneath the base of the right one. Eyes none. Gill attached to the left side lying across the top of the body just within the mantle edge."

Radula. As noted in the remarks under the genus, the radular illustration and tooth count provided by Bush is incorrect; the radula is probably typical for the genus.

Type localities: For *Choristella leptalea*, off Martha's Vineyard Island, Massachusetts (USFC Sta. 2547), 713 m, 1885. For *C. brychia*, off Martha's Vineyard Island, Massachusetts (USFC Sta. 2234), 1481 m, 1884.

Type material: Holotype, *Choristella leptalea*, USNM 52504 (Figures 25, 26). Although collected alive, the specimen is now broken, the final whorl separated. The label reads "jaw-radula, operculum mounted," but these preparations could not be located.

Holotype, *Choristella brychia*, USNM 77622 (Figures 27–29). The specimen is intact, although the lip is now broken at the base.

Remarks: *Choristella leptalea* is a relatively small-sized member of the family, having a maximum dimension of only 4.0 mm, compared to 10 mm reached by some species. The number of whorls is equal to that of other species, which suggests that it is based on mature specimens. It occurs sympatrically with *C. tenera*, from which it differs in its lower spire.

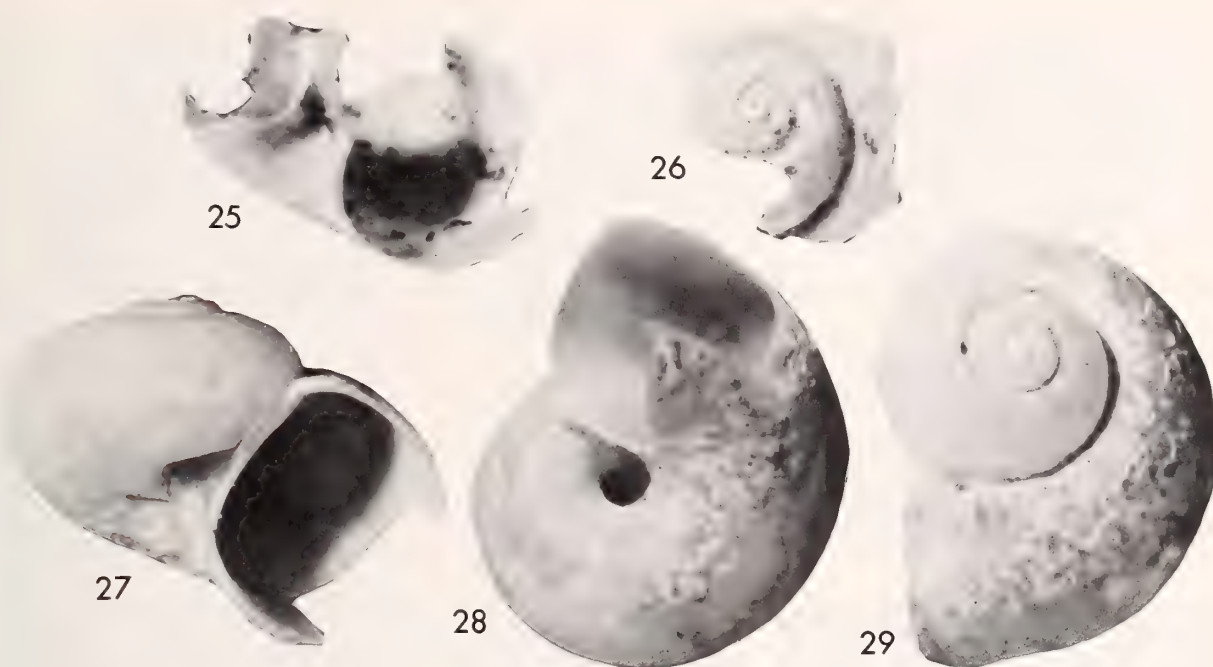
Choristella brychia Bush, 1897, was based on a single specimen. It was described briefly: "This is a larger species of firmer texture than the preceding [*C. leptalea*], although of the same number of whorls. Sculpture none. Color dirty white tinted with brown. Where not worn the surface is slightly lustrous. Interior of aperture very smooth and lustrous, showing a sutural band of delicate rose color." The size difference of 0.5 mm is not sufficient grounds to recognize *C. brychia* as a species distinct from *C. leptalea*. The original figures of the shells are not helpful because an apertural view was used for *C. leptalea*, whereas a spire view was given for *C. brychia*.

Although Bush did not state that the operculum of *Choristella leptalea* is multispiral, her fig. 8 clearly shows 4.5 whorls in a multispiral pattern. The diagnosis above includes mention of periostracum, based on my examination of the holotype of *C. brychia*, although this was not mentioned by Bush. The remains of the holotype of *C. leptalea* show an extremely thin, pale periostracum, not as dark as that of *C. tenera*. The original description of *C. leptalea* does not include mention of the carination that descends within the umbilicus, which is clearly visible on the holotypes of both *C. leptalea* and *C. brychia*.

Choristella ponderi McLean, sp. nov.

(Figures 30–38)

Description: Shell (Figures 30–33) small for genus (maximum diameter 4.7 mm), spire height relatively low (height–



Explanation of Figures 25 to 29

Figures 25–29. *Choristella leptalea* Bush, 1897. Figures 25, 26. Holotype, USNM 52504, off Martha's Vineyard Island. Original height 2.5 mm (BUSH, 1897). Figure 25, broken remains of aperture. Figure 26, broken remains of spire. Figures 27–29. Holotype of *Choristella brychia* Bush, 1897, USNM 77622, off Martha's Vineyard Island. Height 3.1 mm. Apertural, basal, and oblique spire views.

width ratio of holotype 0.68). Shell wall extremely thin. Surface shiny, white, periostracum thin, colorless. Protoconch (Figure 36) tip bulbous, surface smooth. Teleoconch whorls 3, rounded, smooth, suture deeply impressed. Umbilicus narrow, deep, not obstructed by reflection of inner lip, inner extent of umbilicus defined by narrow ridge. Spiral sculpture represented only by umbilical ridge; axial sculpture lacking, except for fine growth increments. Peristome complete, area of contact with previous whorl minimal; lip flared below, broadest at base of columella, where buttressed by umbilical ridge. Operculum (Figure 34) pale brown, nucleus slightly excentric, final whorl rapidly expanding to produce paucispiral pattern.

Dimensions. Height 3.2 mm, width 4.7 mm (holotype); height 3.5 mm, diameter 4.7 mm (figured specimen, AMS C.155463).

External anatomy (Figure 37). The mouth is bordered laterally by projecting oral lappets. No groove on the right tentacle was detected, but the specimen may be female.

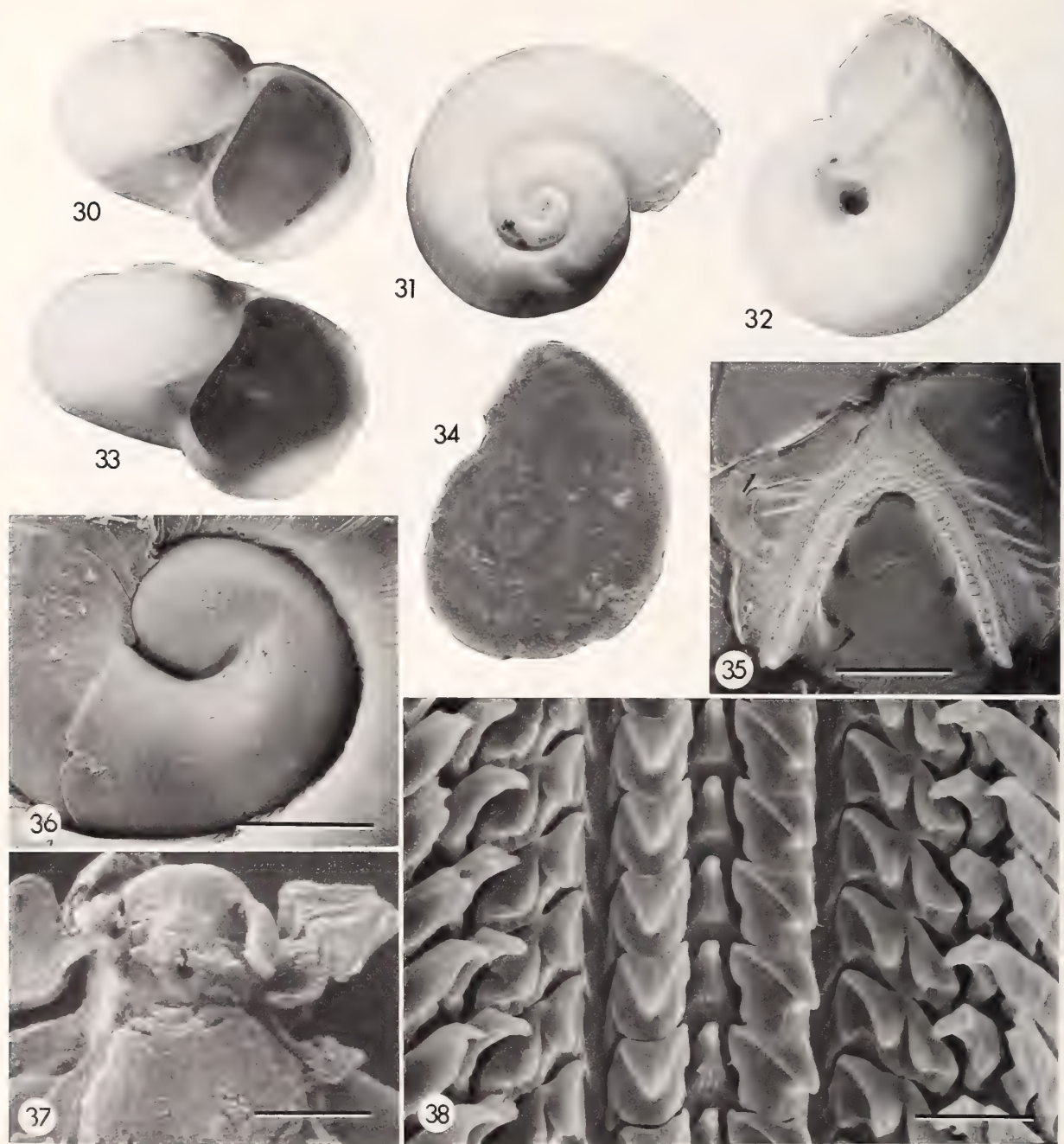
Jaw (Figure 35). As described for genus.

Radula (Figure 38). The radula agrees with that given for the family. The rachidian is unusual in the genus in seeming to have three projecting nubs at the base of the shaft.

Type locality: Off Sydney, New South Wales, Australia (33°47.5'S, 151°28.5'E), 124 m, in skate egg case.

Type material: 6 specimens from type locality, R/V *Kapala* Sta. K86/14/16, 2 July 1986. Holotype and paratypes AMS C.151524, bodies preserved separately. Ten additional paratypes, off Shoalhaven Heads, N.S.W. (34°56'S, 151°9.5'E), 494–585 m, in elasmobranch egg cases, R/V *Kapala* Sta. K86/23/04, 10 September 1986, small to medium-sized specimens with dried bodies, 3 specimens wet-preserved; distribution: 6 paratypes AMS C.167692; 1 paratype LACM 2630, 2 paratypes NMNZ, 1 paratype MNHN.

Referred material (arranged north to south): AMS C.155457, NE of North Reef, Queensland (23°08.4'S, 152°12.3'E), R/V *Kimbla* Sta. 20, 14 December 1977, 1 dead specimen. AMS C.155458, E of North West Island, Queensland (23°19.5'S, 152°35.4'E), 320 m, R/V *Kimbla* Sta. 23, 14 December 1977, 1 dead specimen. AMS C.155462, E of Lady Musgrave Island, Queensland (23°33.7'S, 152°37.0'E), 339 m, R/V *Kimbla* Sta. 3, 17 November 1977, 1 dead specimen. AMS C.155459, NE of Lady Musgrave Island, Queensland (23°38.8'S, 152°45.5'E), 365 m, R/V *Kimbla* Sta. 24, 14 December 1977, 4 small dead shells. AMS C.155461, E of Lady Musgrave Island, Queensland (23°44'S, 152°49'E), 357 m, R/V *Kimbla* Sta. 2, 17 November 1977, 1 dead specimen. AMS C.151990, E of Lady Musgrave Island, Queensland (23°52.2'S, 152°42.2'E), 296 m, R/V *Kimbla*



Explanation of Figures 30 to 38

Figures 30–38. *Choristella ponderi* McLean, sp. nov. Figures 30–32. Holotype, AMS C.151524, off Sydney, New South Wales, Australia. Height 3.2 mm. Apertural, spire, and umbilical views. Figure 33. AMS C.155463, off Fraser Island, Queensland, Australia. Height 3.5 mm. Figure 34. SEM view of operculum of paratype, AMS C.151524. Scale bar = 1 mm. Figure 35. SEM view of jaw of paratype, AMS C.151524. Scale bar = 200 μ m. Figure 36. SEM view of early whorls, showing protoconch and first teleoconch whorl. SEM photo by B. Marshall. AMS C.82431, off Caloundra, Queensland. Scale bar = 100 μ m. Figure 37. SEM view of critical point dried body, showing cephalic tentacles, oral lappets, and foot with pedal gland, paratype, AMS C.151524. Figure 38. SEM view of radula, paratype, AMS C.151524. Scale bar = 25 μ m.

Sta. 15, 7 July 1984, 3 dry specimens. AMS C.155460, off Frazer Island, Queensland (24°57.9'S, 153°37.3'E), 210 m, R/V *Kimbla* Sta. 27, 15 December 1977, 1 small dead specimen. AMS C.155463, S end Fraser Island Queensland (27°57'08"S, 153°51'03"E), 201 m, R/V *Kimbla* Sta. Q13, 10 November 1976, 1 dry specimen (Figure 33). AMS C.150125, N of Coolongatta, Queensland (28°07'S, 153°50'E), 146 m, R/V *Kapala* Sta. K78-17-14, 18 August 1978, 1 small specimen. AMS C.82431, E of Caloundra, Queensland, 91–110 m (50–60 fm), T. A. Garrard Coll., 1 specimen (Figure 37, protoconch). AMS C.150127, off Kiama, N.S.W. (34°46'S, 151°13'E), 387–552 m, in egg case, R/V *Kapala* Sta. K86-09-03, 15 April 1986, 2 small specimens, dry shells and wet bodies separate.

Remarks: This species is characterized by its small size, low spire, and relatively few whorls. There are a sufficient number of records to be certain that the specimens are mature. In its small size and low spire it is most similar to *Choristella leptalea* Bush, a species too poorly known to allow full comparison.

Choristella ponderi is broadly distributed on the east coast of Australia. Records are known from Queensland (23°08'S) to New South Wales (34°56'S).

Etymology: The name honors Winston Ponder, of the Australian Museum, Sydney.

Choristella hickmanae McLean, sp. nov.

(Figures 39–45)

Choristella n. sp.: HICKMAN, 1983:86, fig. 29 [radula].

Description: Shell (Figures 39–43) large for genus (maximum diameter 9 mm), spire height relatively low (height-width ratio of holotype 0.72). Shell wall extremely thin, maximum thickness of broken lip 0.1 mm. Surface dull, yellowish white, periostracum not evident, surface finely pitted. Protoconch and earliest teleoconch whorl missing. Remaining whorls 3.5, rounded, smooth; suture deeply impressed. Umbilicus broad, deep, not obstructed by reflection of inner lip. Spiral sculpture represented only by single narrow ridge deep within umbilicus; axial sculpture lacking, growth increments not apparent. Peristome complete, area of contact with previous whorl minimal. Operculum (Figure 39) pale brown, nucleus slightly excentric, final 3 whorls evenly expanding in multispiral pattern.

Dimensions. Height 6.5 mm, width 9.0 mm (estimated dimension of holotype prior to breakage); height 7 mm, diameter 10 mm (estimated dimension of sectioned paratype).

External anatomy. Figure 44 shows the left (umbilical view) side of a paratype specimen prior to sectioning. Four epipodial tentacles are shown adjacent to the operculum.

Radula (Figure 45). The radula agrees with the generic description in its overall morphology. The rachidian tooth

has a weakly projecting shaft, but a small, clearly distinct, overhanging cusp.

Type locality: Northern Cascadia Abyssal Plain, at base of continental slope, 95 nautical miles (172 km) west of Strait of Juan de Fuca, Washington (48°38.1'N, 126°58.0'W), 2176 m, gray silty clay. CAREY (1981) described the bottom conditions for the Cascadia Abyssal Plain.

Type material: 3 specimens from type locality, all with damaged shells, collected with beam trawl by A. Carey, Oregon State University (BMT-DWD Sta. 9), 11 September 1971. Holotype, LACM 2249 (Figures 42, 43) body used for light microscope preparation of radula. Two paratypes, LACM 2250, one sectioned, shell destroyed, photograph of shell and body prior to sectioning (Figures 39–41), one paratype specimen with badly damaged shell used for SEM preparation of radula by C. Hickman (Figure 45).

Remarks: *Choristella hickmanae* is a relatively low-spined species comparable to *C. leptalea* and *C. ponderi*, but is larger than either species (9 mm maximum dimension, compared to 4.0 mm for *C. leptalea* and 4.7 mm for *C. ponderi*). Each species has 3.5 whorls. The umbilicus of *C. hickmanae* is broader than that of *C. leptalea* and *C. ponderi*, in which the peristome is slightly reflected over the umbilicus.

The fine pitting on the surface of the shell is probably a result of etching due to the original preservation in formalin.

There is no record of association of the type lot with shark or skate egg cases, but the extremely thin shell and damaged condition of all specimens suggest that protection within an elasmobranch egg case would be essential to this species.

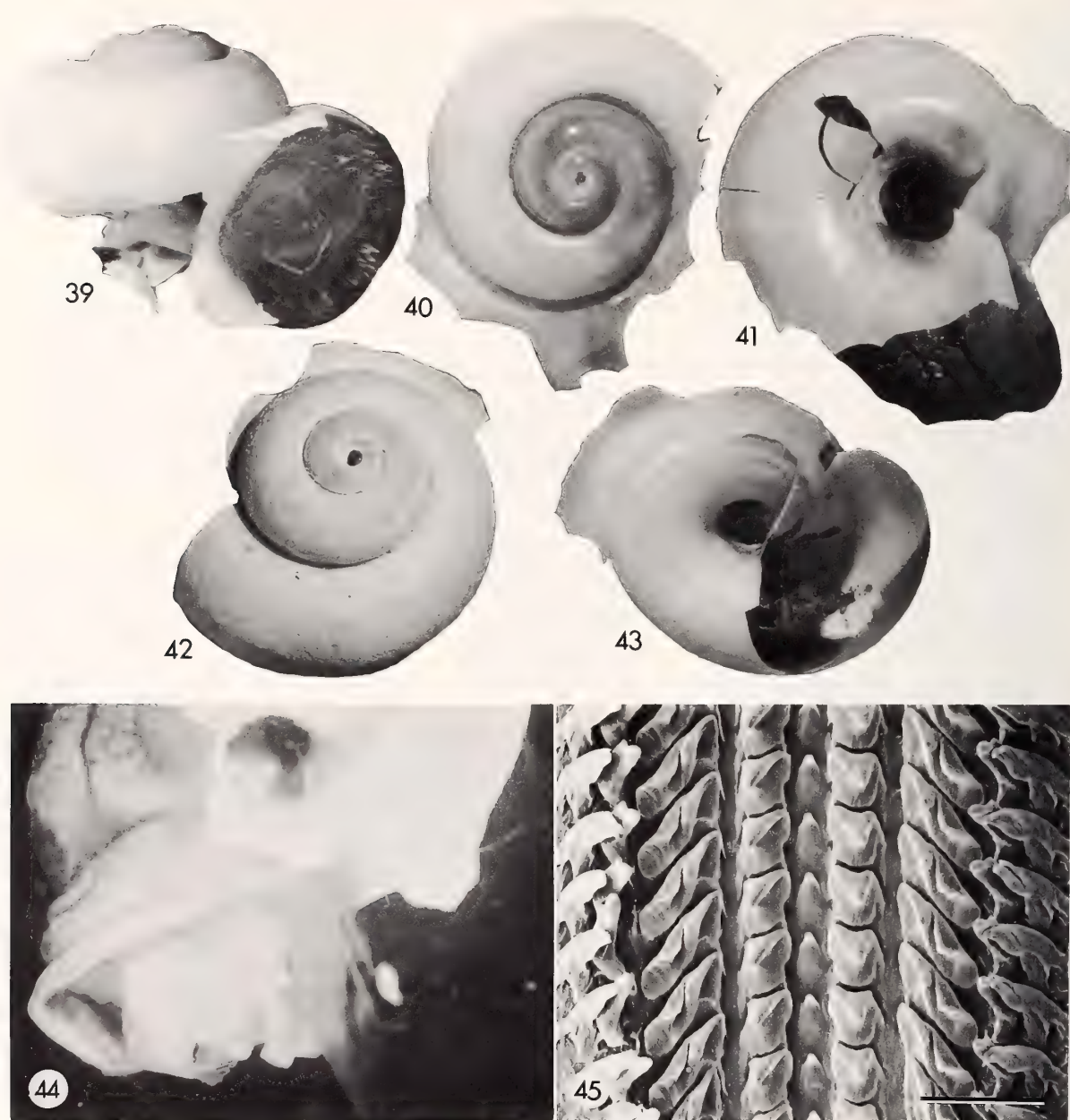
Etymology: This species is named after Carole S. Hickman, University of California, Berkeley.

Further Records of *Choristella* spp.

Four additional lots of *Choristella* species from the MNHNP collection were received on loan from P. Bouchet subsequent to the initial submission of this paper. All represent immature specimens and I refrain from describing further new taxa from this material because mature examples are unknown. These lots are listed here:

MNHN uncataloged, Mozambique Channel (11°44'S, 47°35'E), 3716 m. R/V *Suroit*, BENTHEDI Expedition, Sat. 87, 3 April 1977. Five specimens, maximum diameter 2.0 mm. Specimens of 1.0 mm in diameter show a basal carination.

MNHN uncataloged, Norfolk Ridge (23°03'S, 167°19'E), 503 m. R/V *N. O. Vauban*, SMIB 3 Expedition, Sta. DW22, 24 May 1987. Two specimens, maximum



Explanation of Figures 39 to 45

Figures 39–45. *Choristella hickmanae* McLean, sp. nov. Figures 39–41, 44. Paratype specimen prior to sectioning, Northern Cascadia Abyssal Plain off Washington, LACM 2250. Height 6.5 mm (estimate). Figures 42, 43. Holotype, same locality, LACM 2249. Diameter of broken shell 8.0 mm. Figure 45. SEM view of radula of paratype, LACM 2250. Scale bar = 50 μ m.

diameter 2.0 mm. Shell profile low, not showing basal carination. Radula and jaw examined with SEM, typical for *Choristella*.

MNHN uncataloged, Tanimbar Islands, Indonesia (08°42'S, 131°54'E), 356–368 m. R/V *Baruna Jaya 1*, KARUBAR expedition, Sta. CP69, 2 November 1991. Six specimens, maximum diameter 3.5 mm. Shell profile of

medium height; small specimens not showing basal carination. Radula and jaw examined with SEM, typical for *Choristella*.

MNHN uncataloged, Kai Islands, Indonesia (06°08'S, 132°45'E), 390–502 m, R/V *Baruna Jaya 1*, KARUBAR expedition, Sta. CP35, 27 October 1991. One specimen, maximum diameter 4.0 mm, similar to preceding lot.

Bichoristes McLean, gen. nov.

Type species: *Bichoristes wareni* McLean, sp. nov.

As the genus is monotypic, the generic diagnosis and remarks are combined in the species treatment below.

Bichoristes wareni McLean, sp. nov.

(Figures 46–53)

Description: Shell (Figures 46–48) minute (maximum diameter 3.2 mm), thin, periostracum unknown, whorls 3.2, quadrangular in section, growth form planispiral with two acutely angled, projecting carinations at outer edge, one above and the other below position of protoconch; upper carina projecting slightly more than lower carina. Suture at position of upper carination of previous whorl, not channeled; whorl extending above suture, forming rounded angulation, base defined at position of broadest possible umbilicus by sharp angulation. Spiral sculpture lacking except for these four carinations. Axial sculpture of exceedingly fine growth increments, prosocline on upper surface of whorl, greatest curvature close to suture, opisthocline on outer surface between the two keels, prosocline on base, greatest curvature close to umbilical keel. Aperture quadrangular, peristome complete; mature upper lip, outer lip, and lower lip slightly flared. Protoconch (Figure 49) diameter 200 μ m, tip bulbous, surface smooth, visible equally in spire and umbilical views, similarly recessed in both views. Operculum (Figure 50) thin, multispiral, about 10 whorls visible.

Dimensions. Height 1.4 mm, diameter 3.2 mm (holotype); height 1.2 mm, diameter 3.0 mm (paratype).

External anatomy. Unknown.

Jaw (Figure 51). Typical for family.

Radula. (Figures 52, 53). Rachidian tooth relatively large, with triangular shaft and prominent overhanging cusp; base of shaft with lateral nubs and one central nub. First lateral tooth massive, with two cusps, the innermost small and blunt like that of rachidian, the outermost acutely triangular and with long overhang; shaft base articulating with tooth below, inner edge of shaft articulating with rachidian. Second lateral tooth largest in row, with single large acutely pointed overhanging cusp, its upper profile descending away from rachidian, shaft long and deeply excavated for accommodation of outer lateral teeth. Third lateral tooth with long shaft and pointed cusp that projects over the deeply excavated shaft of second lateral tooth. Fourth lateral tooth small, fused with and emerging from shaft of third. Fifth lateral tooth vestigial, a small flap at the base of the shaft of the third lateral tooth.

Type locality: Norfolk Ridge, S of New Caledonia (24°55'S, 162°22'E), 505–515 m.

Type material: Holotype MNHN uncataloged, from type locality, R/V *Jean Charcot*, BIOCAL Expedition Sta. DW66, 3 September 1985. The body of the specimen was

extracted through a hole filed in the shell by A. Warén, who examined the operculum, radula, and jaw with SEM and provided the prints used here. One paratype, MNHN uncataloged, Norfolk Ridge (23°03'S, 167°19'E), 503 m, R/V *N. O. Vauban*, SMIB 3 Expedition Sta. DW22, 24 May 1987.

Remarks: The discovery of a planispirally coiled member of the Choristellidae was unanticipated. Although the shell morphology seems to be completely different from that of other choristellids, there are a number of shared characters: (1) shell is extremely thin; (2) protoconch surface is smooth; (3) teleoconch whorls do not exceed 3.5; (4) contact with the previous whorl is limited to the thin layer that makes the peristome complete where it fuses with the parietal wall, and (5) the umbilicus is as broad as is physically possible, the inner basal keel of *Bichoristes* corresponding to the sharp umbilical ridge of *Choristella*. *Bichoristes* adds the outer two keels; these delimit the area of contact for the next whorl, and the result is a planispiral growth form.

The radula has the basic choristellid plan, differing from that of *Choristella* in having the first rather than second lateral tooth the bicuspid tooth. Other distinctions are the nubs at the base of the shaft of the rachidian and the fusion of the fourth lateral tooth with the third.

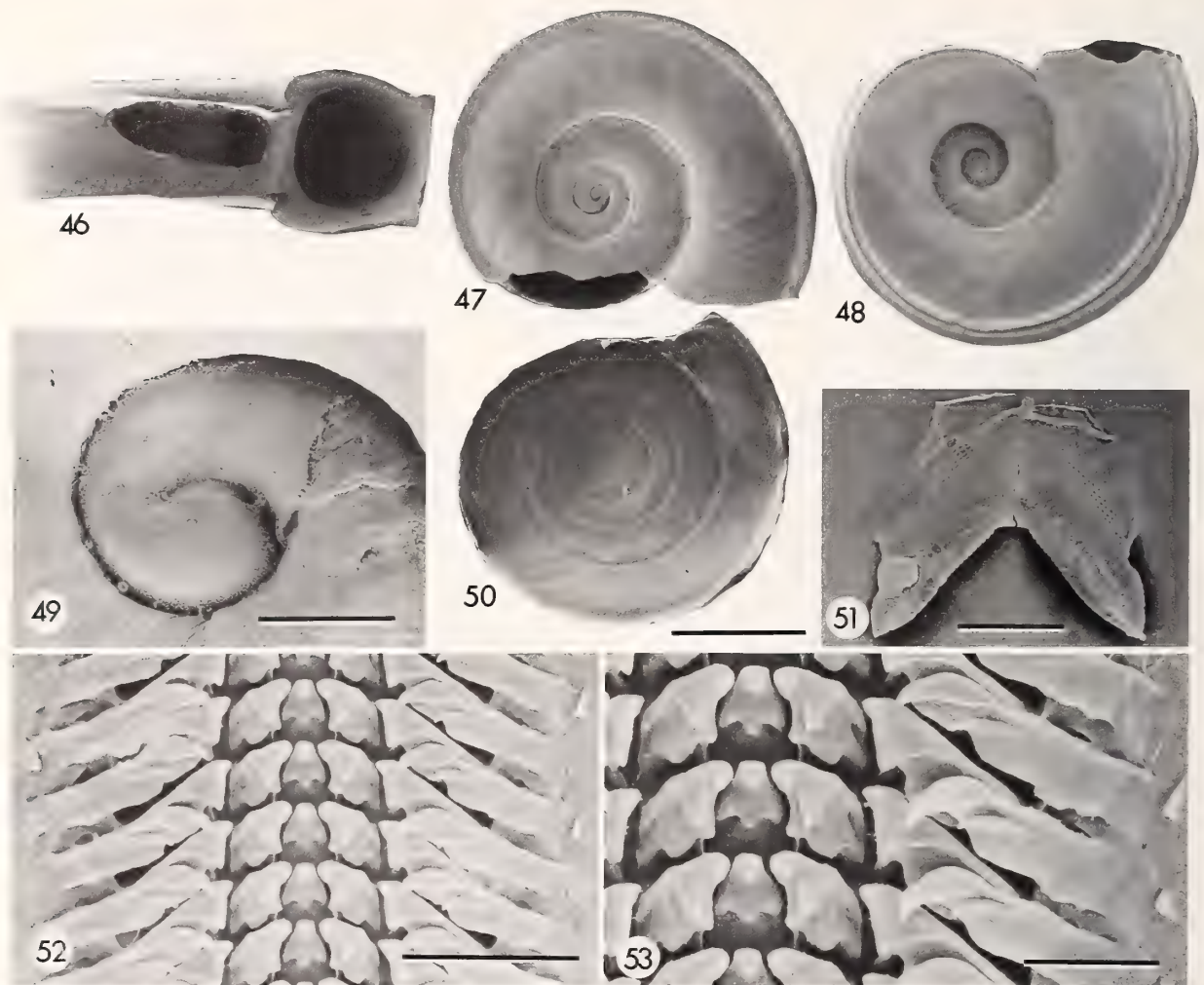
The sculptured shell of *Bichoristes* has to be interpreted as either derived or primitive in the family. I interpret *Bichoristes* as derived from the low-spined shell form typified by *Choristella ponderi* by the not so extreme modifications to the sculpture noted above. Its jaw and radula are so like those of other choristellids that it is difficult to conceive of a differing life mode. Functionally, its quadrangular shell morphology provides structural support. The narrow planispiral shell form would enable access to the deep crevices at both ends of the elasmobranch egg case, where a planispiral shell could be expected to penetrate further than the helically coiled shell form of *Choristella*.

Etymology: The name honors Anders Warén, of the Swedish Museum of Natural History, Stockholm, who recognized the familial affinity of the species among material in the MNHN collection.

DISCUSSION

Choristellidae and Addisoniidae share many characters of internal anatomy (HASZPRUNAR, 1988c, 1992) and a similar habitat and feeding specialization on the spent egg cases of elasmobranchs. Members of both families are thin-shelled, affording little protection from predators; instead, protection is provided by the thick walls of the egg cases within which they live.

The radula in the Choristellidae and Addisoniidae is relatively large and is provided with robust teeth that are capable of gouging into the walls of the egg cases to provide a direct source of food. Marshall (personal communication) reports that the inner wall of egg cases that contained



Explanation of Figures 46 to 53

Figures 46–53. *Bichoristes wareni* McLean, sp. nov. All are SEM views of holotype specimen, MNHN, Norfolk Ridge. Diameter 3.2 mm. Figures 46–48. Apertural, spire, and umbilical views. Figure 49. Protoconch. Scale bar = 100 μ m. Figure 50. Operculum. Scale bar = 400 μ m. Figure 51. Jaw. Scale bar = 100 μ m. Figure 52. Radula. Scale bar = 20 μ m. Figure 53. Radula. Scale bar = 10 μ m.

Choristella marshalli were eaten by the limpets. McLEAN (1985) illustrated radular grazing marks made on the inner wall of an egg case by *Addisonia brophyi* McLean, 1985.

The radula in other cocculiniform families is relatively small with weakly developed teeth in the central field; most of these families also differ in having marginal teeth that are used for sweeping. MARSHALL (1986) has emphasized that the diet in these families is likely the bacteria that are associated with the decomposition of the biogenic substrates, rather than the direct food source provided by the substrate.

There is no indication that members of either the Choristellidae or Addisoniidae occur in the capsules of developing elasmobranchs. The thin-shelled mollusks would be exposed to predators during penetration of the egg case. Thus

it is incorrect to say that these mollusks are parasitic. Dispersal of these mollusks would necessarily be possible only during the larval stage, at which time the larvae would settle on and enter a spent capsule through the opening from which the young elasmobranch had emerged.

Sizes of the egg cases available in the benthos places limits on the maximum size attained by choristellid and addisoniid species. The maximum size of 10 mm in choristellids could only be exceeded if the elasmobranch capsule were unusually large.

The distribution of each species must depend upon the availability of egg cases of sharks and skates. As noted earlier (McLEAN, 1985), egg cases are produced by three elasmobranch families, the cat sharks (family Scyliorhinidae), with about 85 species in the world, the bullhead or

horn sharks (family Heterodontidae) and the skates (family Rajidae) (ESCHMEYER *et al.*, 1983). COX (1963) and ESCHMEYER *et al.* (1983) illustrated the egg cases of the species in these families known from California. If a worldwide study of capsule producing elasmobranchs were available, it would be possible to predict the likelihood of associated species of choristellids and addisoniids. Because too few records are currently known, it is unknown whether choristellid species are host specific.

WOURMS (1977) reviewed the literature on elasmobranch egg-case structure and formation. Egg cases are composed of layers of the structural protein collagen, which exhibits unique chemical and physical properties when deployed in the egg cases. Shark embryos develop within the egg cases for up to nine months, during which there is little evidence of deterioration of the egg cases. The duration of spent egg cases in the benthos is unknown, nor am I aware of their being used as food by other organisms, but the cases undoubtedly persist in the benthos for a number of years. The egg cases should therefore provide a persistent and reliable food source.

SUMMARY

Additions to knowledge of the Choristellidae that result from this study are:

(1) Family-level shell characters are minute to small size, extremely thin shell, complete peristome, deep suture (except *Bichoristes*), umbilical ridge, smooth bulbous protoconch, and maximum of 3.5 teleoconch whorls.

(2) The radula is unique to the family. Its resemblance to that of the Cocculinellidae is superficial.

(3) The bulbous protoconch tip is unlike the compressed, laterally pinched protoconch tip of Pseudococculinidae and Cocculinellidae. Protoconch characters may yet confirm the affinity to Addisoniidae suggested by anatomical characters (HASZPRUNAR, 1992), but have not helped because the protoconch of Addisoniidae is deciduous and remains unknown.

(4) Taxa based on shell characters can readily be excluded from the genus if they do not meet all these criteria. In the Appendix, 10 species-level taxa that have previously been assigned to the family are excluded. Skeneiform genera with a sharp umbilical ridge may be excluded by lacking the deep suture.

(5) Specific characters in *Choristella* are relative size, relative proportions of height to width, and whether the multispiral operculum looks multispiral or appears to be paucispiral as a result of having only three whorls. External anatomy is too poorly known to be useful at this time.

(6) The new genus *Bichoristes* has a uniquely bicarinate and planispiral shell, although the radula is close to that of *Choristella*. Most of the shell characters diagnostic for *Choristella*, including thin shell, 3.5 whorls, smooth protoconch, and umbilical ridge, are present.

(7) Although most species are allopatric, one sympatric pair is known: *Choristella tenera* and *C. leptalea*.

(8) No species is known to be free living and unassociated with the spent egg cases of elasmobranchs.

(9) Shell size is limited by the size of available egg capsules.

(10) The family is broadly distributed, having been found in the most extensively sampled regions of the world in temperate zones at continental shelf to abyssal depths.

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APPENDIX—TAXA EXCLUDED FROM CHORISTELLIDAE

A number of taxa have been incorrectly allocated to the family Choristellidae (originally assigned to the “Choristidae”). The following taxa have not been shown to have the choristellid radular plan and lack some or all of the diagnostic shell characters (small size, extremely thin shell, complete peristome, deep suture, and sharp carination descending into the umbilicus). Some of the misallocated taxa are naticids, but many are potential members of the family Skeneidae (superfamily Trochacea). Skeneidae and families of similar appearance have been poorly understood but have received recent attention from MARSHALL (1988), HICKMAN & MCLEAN (1990), and WARÉN (1991, 1992). It is beyond the scope of this paper to allocate the following taxa, although some suggestions are made.

1. *Choristes elegans* Carpenter, 1872 (Figure 54)

Choristes elegans Carpenter in DAWSON, 1872:392, pl. 7, figs. 13, 13a; VERRILL, 1882:542, p. 58, fig. 28 [“I have figured a young fossil specimen for convenient comparison”]; RICHARDS, 1962:79, pl. 17, fig. 15 [“Montreal, Pleistocene”]; CLARKE, 1961:360 [in list of species under *Choristes*]; MARINCOVICH, 1977:338 [as valid genus and species of Naticidae]; BOUCHET & WARÉN, 1979, fig. 47 [syntype]. Type locality: Pleistocene, St. Lawrence River Estuary, Montreal, Quebec. **Lectotype (here designated):** USNM 188948; 2 paralectotypes: USNM 56385.

Carpenter was uncertain as to the familial relationships of the Pleistocene fossil he described as *Choristes elegans*: “It is hard to pronounce satisfactorily on its relationships. In its thin, coated shell it resembles *Velutina*; the striae and loose whirls recall *Naticina*; the straight pillar lip reminds us of *Fossarus*; while the umbilicus and rounded base, with entire mouth, best accord with the *Natica* group.”

Although MARINCOVICH (1977) used *Choristes* for eastern Pacific naticid species, he cited only the original illustration of the type species; it is not clear whether he examined specimens. He did not cite the illustration of RICHARDS (1962:79, pl. 17, fig. 15), who figured a specimen identified as *Choristes elegans* from the Montreal Pleistocene and placed it in Choristidae without comment. BOUCHET & WARÉN (1979) figured a syntype without citing a catalog number. There are three shells in the USNM collection labeled *Choristes elegans* Carpenter, “Postpliocene, Montreal, Dawson.” A **lectotype** (USNM 188948, height 20.1 mm, Figure 54) and two **paralectotypes** (USNM 56385, heights 16.7 mm and 17.2 mm) are

here designated. The lectotype (Figure 54) shows irregular spiral sculpture and the inner lip detached from the parietal wall. Carpenter noted the “smooth epidermis lining the umbilical chambers, conspicuously preserved, even in these fossil specimens, between the closest part of the parietal region.”

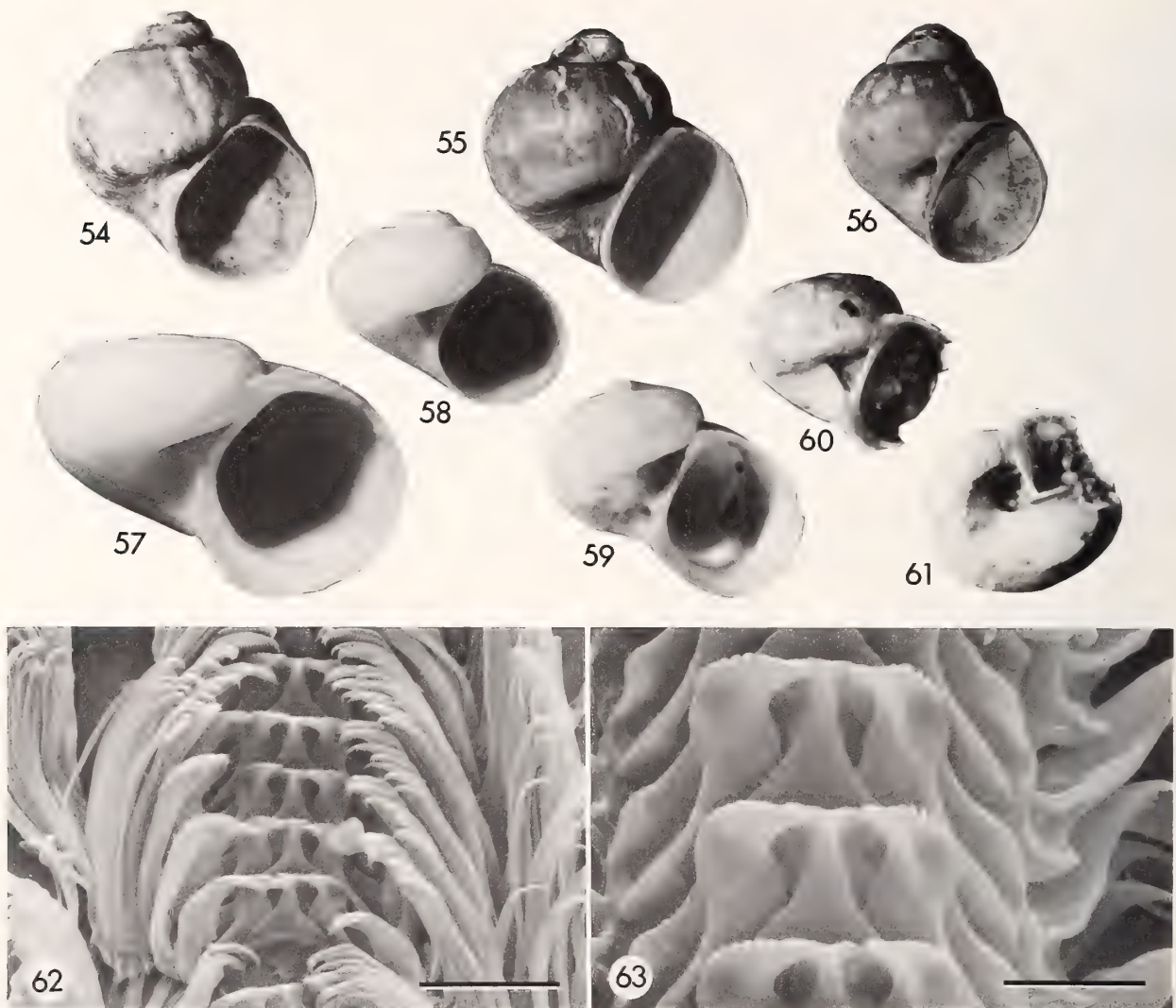
The type material of *Choristes elegans* is here identified as a variation of the naticid *Amauropsis islandica* (Gmelin, 1791), a morphologically variable species that is broadly distributed in shallow to moderate depths in the North Atlantic and Arctic Oceans. In his redescription of *A. islandica*, MARINCOVICH (1977:217, pl. 17, figs. 1–4, pl. 22, fig. 1) described the umbilicus as “open, extremely narrow and slitlike, usually concealed by periostracum of inner lip margin.” This description of the periostracum agrees with that of Carpenter for *Choristes elegans*. The three specimens have broader umbilici than most specimens of *A. islandica*, but such a shell form may possibly correlate with the lowered salinity in the estuary of the St. Lawrence River.

MARINCOVICH (1977:338) was the first subsequent author to correctly assign *Choristes* to the Naticidae. GOLOKOV & STAROBOGATOV’s (1975) assignment to the Naticidae on radular characters cannot be credited because it could only have been based on published illustrations of the radula of “*Choristes*” *tenera* (which is not a naticid). However, Marincovich did not note the fact that *Choristes elegans* would have to be considered extinct if recognized as a valid species; he did not compare it to *Amauropsis islandica* and he did not conclude that *Choristes tenera* Verrill should be assigned elsewhere, despite noting that the radular dentition of that species differed from that of two Recent naticids he assigned to *Choristes*. Instead, he stated that “another radular mount should be made to confirm the radular dentition reported by VERRILL (1882).”

KABAT (1989, 1991) was aware that Choristellidae Bouchet & Warén, 1979, solved the nomenclatural problem for the choristellids, but pointed out that Choristidae Verrill, 1882 (Naticacea) presented a problem of homonymy for the well-known insect family Choristidae Esben-Petersen, 1915 (nominotypical genus *Chorista* Klug, 1836). Kabat proposed that Choristidae Verrill be emended to Choristeidae Verrill, to conserve Choristidae Esben-Petersen and to retain Choristeidae in the event that it might prove to have utility in the Naticacea. Kabat (personal communication) now agrees with the synonymization of *Choristes* with *Amauropsis*.

2. *Choristes carpenteri* Dall, 1896 (Figures 55, 56)

Choristes carpenteri DALL, 1896:10; DALL, 1908:328, pl. 3, fig. 4; KEEN, 1971:388, fig. 424 [copy fig. of DALL, 1908]; CLARKE, 1961:360 [in list of *Choristes* species]; MARINCOVICH, 1977:340, pl. 31, figs. 8, 9, text fig. 11b [radula]. Type locality: Gulf of Panama, 2693 m. Holotype: USNM 123039.



Explanation of Figures 54 to 63

Figures 54–63. Type specimens of taxa incorrectly referred to Choristellidae. Name combinations as originally proposed. Figure 54. Lectotype, *Choristes elegans* Carpenter, 1862. USNM-56385. Pleistocene, St. Lawrence River Estuary, Montreal, Quebec. Height 20.1 mm. Figure 55. Holotype, *Choristes carpenteri* Dall, 1896. USNM 123039. Gulf of Panama, 2693 m. Height 21.0 mm. Figure 56. *Choristes carpenteri*, second reported specimen, USNM 123038. Gulf of Panama, 2690 m. Figure 57. Holotype, *Cyclostrema pompholyx* Dall, 1889. USNM 214279. Gulf of Mexico, 1472 m. Diameter 4.1 mm. Figure 58. Holotype, *Choristes agulhasae* Clarke, 1961. MCZ 224955. Cape Basin off South Africa, 4585 m. Height 2.0 mm. Figure 59. Holotype, *Choristes agulhasae argentinae* Clarke, 1961. Argentine Basin, 5130 m. MCZ 224956. Height 2.3 mm. Figures 60, 61. Syntype, *Cithna naticiformis* Jeffreys, 1883. BMNH 85.11.5.1615–1617. Porcupine Expedition of 1870, Sta. 17a, off Portugal, 1353 m. Height 1.8 mm. Specimen is still attached to cardboard mount. Figures 62, 63. SEM views of radula from holotype of *Choristes agulhasae* Clarke, 1961, courtesy B. Marshall. See text for generic assignment to *Trenchia* Knudsen, 1964. Scale bar of Figure 62 = 100 μ m, of Figure 63 = 40 μ m.

Despite the fact that *Choristes* was based on a shallow-water type species, MARINCOVICH (1977) retained the genus for two abyssal, eastern Pacific naticid species, *Choristes carpenteri* Dall, 1896, and *C. coani* Marinovich, 1975, invoking a unique radular definition ("monocuspate rachidian, one monocuspate lateral, and two monocuspate

marginal teeth per half row"). Now that *Choristes* is relegated to the synonymy of *Amauropsis*, these two species are in need of generic reassignment in Naticidae. Affinity to *Amauropsis* is ruled out, as its type species has a tricusate rachidian tooth.

The holotype of *Choristes carpenteri* (USNM 123039,

from USFC Sta. 3382), is 21 mm in height, which is sufficiently large to remove it from consideration as a member of the Choristellidae. No mention of an operculum was made in the original account and the specimen appears not to have been collected alive. This specimen has the apical area worn. It is illustrated here for the first time (Figure 55).

In his subsequent account DALL (1908) mentioned a second specimen, from USFC Sta. 3361, 2690 m, Gulf of Panama. This must have been the specimen to which he referred in reporting that "the animal agrees in general appearance with that of *Choristes elegans* var. *tenera* Verrill, as described by Verrill." This specimen, USNM 123038, from USFC Sta. 3361 (Figure 56) is also marked "type"; it measures 15.0 mm in length. It exhibits a characteristic sculptural pattern of naticids in having collabral ridges on the upper part of the whorl near the suture. This specimen has the operculum and a dried body, but the body does not have the epipodial tentacles that may be seen on the dried bodies of *Choristella tenera*. Clearly and inexplicably Dall erred in reporting that the animal agreed with Verrill's species. Although MARINCOVICH purported to figure the holotype (1977:fig. 8), he actually figured this second specimen mentioned by Dall (USNM 123038), and incorrectly gave the length at 20.5 mm, rather than 15.0 mm.

3. *Choristes coani* Marinovich, 1975

Choristes coani MARINOVICH, 1975:169, figs. 2, 6, 7; MARINOVICH, 1977:341, pl. 31, figs. 10–12, text fig. 11c [radula]. Type locality: off Central Oregon, 2830 m. Holotype: USNM 741014.

This was described by Marinovich in the family Naticidae. Like the preceding species, it is in need of generic reassignment.

4. *Cyclostrema pompholyx* Dall, 1889 (Figure 57)

Cyclostrema pompholyx DALL, 1889:394, pl. 28, fig. 9; BUSH, 1897:139; TURNER, 1978:17, figs. 11, 12. Type locality: Gulf of Mexico, 1472 m. Holotype: USNM 214279.

Choristes pompholyx: CLARKE, 1961:360 [in list of *Choristes* species].

DALL (1889) originally stated: "I am in doubt as to the generic place of this species, so simple in its characters and without the soft parts. I had thought of putting it under *Choristes* or with *Vitrinella*, and finally in placing it here [*Cyclostrema*] feel by no means satisfied that the choice is a correct one." BUSH (1897) noted that Dall's species "may prove to be another species of *Choristes*," accounting for CLARKE (1961) having placed it in *Choristes*.

The shell is sturdy with a broadly inflated lip. It lacks the umbilical ridge of *Choristella*. There is no evidence to support the allocation of this species to the family Choristellidae.

5. *Choristes agulhasae* Clarke, 1961 (Figure 58)

Choristes agulhasae CLARKE, 1961:361, pl. 3, fig. 1. Type locality: Cape Basin (corrected from Agulhas Basin), SW of Cape Town, South Africa, 4585 m. Holotype: MCZ 224955.

No evidence was advanced to support the assignment of this species to the family, although there is an umbilical carination similar to that of *Choristella*. The radula (Figures 62, 63, SEM photos by Bruce Marshall) is rhipidoglossate, unlike that of Choristellidae. Marshall (personal communication) has identified it as that of *Trenchia* Knudsen, 1964 (family Skeneidae), characterized by the elongate and laterally excavated base of the first lateral tooth.

6. *Choristes agulhasae argentinae* Clarke, 1961 (Figure 59)

Choristes agulhasae argentinae CLARKE, 1961:361, pl. 3, figs. 2, 3. Type locality: Argentine Basin, ESE of Buenos Aires, Argentina, 5130 m. Holotype: MCZ 224956.

The holotype (Figure 59) is a single empty shell, larger than that of the preceding taxon. No evidence supports assignment to Choristellidae. It may be regarded as a possible member of *Trenchia*.

7. *Cithna naticiformis* Jeffreys, 1883 (Figures 60, 61)

Cithna naticiformis JEFFREYS, 1883:112, pl. 20, fig. 11; WARÉN, 1980:21; GUBBIOLI & NOFRONI, 1986:204, figs. Type locality: Porcupine Expedition of 1870, Sta. 17a, off Cape Mondego, Portugal, 1353 m. Syntypes: 3 shells, BMNH 85.11.5.1615–1617.

GUBBIOLI & NOFRONI (1986) incorrectly used this name for *Choristella nofronii* described here, as detailed in the remarks that follow the new species description. A syntype specimen is illustrated here (Figures 60, 61). Although radular material is not available, it is also a possible species of *Trenchia* on evidence from shell characters.

8. *Cyclostrema valvatoides* Jeffreys, 1883

Cyclostrema valvatoides JEFFREYS, 1883:92; WARÉN, 1980:19; GUBBIOLI & NOFRONI, 1986:205. Type locality: Porcupine Expedition, 1870, Sta. 17a, off Cape Mondego, Portugal, 1353 m. Holotype: BMNH 85.11.5.1593.

GUBBIOLI & NOFRONI (1986) also suggested that this name might apply to *Choristes nofronii* described here. I have examined the holotype, which is in bad condition due to chemical exfoliation; it lacks the umbilical carination of *Choristella*.

9. *Choristes mollis* Okutani, 1964

Choristes mollis OKUTANI, 1964:389. Type locality: off Miyake Island, Japan, 1230–1350 m.

No evidence supported the original placement in *Choristes*. The granular sculpture, and of most importance, the incomplete peristome as illustrated by Okutani are not characters of the family. The operculum is figured as multispiral with more whorls than in species of *Choristella*. Reassignment may be possible if the radula is intact in the holotype. Marshall (personal communication) suggests that it be compared to *Granigyra* Dall, 1889 (family Skeneidae).

10. *Choristes nipponica* Okutani, 1964

Choristes nipponica OKUTANI, 1964:388, pl. 6, fig. 2. Type locality; Sagami Bay, Japan, 1360–1385 m.

No evidence was given to support the assignment of this taxon to *Choristes*. The “shining shell,” sutural shelf rather than channeled suture, produced basal lip, and incomplete peristome are not characters of *Choristella*. The operculum is illustrated as multispiral. Assignment on radular characters may be possible.

On the Anatomy and Relationships of the Choristellidae (Archaeogastropoda: Lepetelloidea)

by

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Abstract. The anatomy of three species of the Choristellidae, *Choristella marshalli*, *C. hickmanae*, and *C. nofronii*, which are described by McLEAN (1992) in the adjoining paper, is described on the basis of reconstructions of serial sections. Choristellids are unique among the lepetelloid Cocculiniformia in having a coiled teleoconch and an operculum as adults. Nevertheless, choristellids can be classified among the Lepetelloidea on anatomical characters. In particular they share the type of gill and the food source (empty egg cases of chondrichthyans) with the addisoniid limpets, although the modifications of the alimentary tract of Choristellidae are unique. Cocculinellidae and Addisoniidae are regarded as the closest relatives of the Choristellidae. Support is given for the hypothesis that teleoconch coiling and gonochorism of the Choristellidae are derived conditions in the Lepetelloidea.

INTRODUCTION

The Choristellidae have been classified in various positions within the Gastropoda. VERRILL (1882:540) placed them among Tectibranchia because of their aberrant “large gill consisting of numerous thin lamellae, attached to the inner surface of the mantle, over the left side of the neck, and extending obliquely across and over the right side.” In contrast, truncatelloid (= rissoacean) affinities were assumed by BUSH (1897:139), THIELE (1929), KURODA *et al.* (1971), and BOSS (1982). The family is based on the genus *Choristella* Bush, 1897 (*Choristes* Verrill, 1882, *non* Carpenter, 1872; see BOUCHET & WARÉN, 1979:225, and McLEAN, 1992).

MOSKALEV (1978) and HICKMAN (1983) noted the similarity of the choristellid radula with the radula of *Cocculinella* Thiele, 1909. In the light of preliminary observations on choristellid anatomy, HASZPRUNAR (1988c) strengthened this proposed relationship and classified the family among the cocculiniform Lepetelloidea closest to the Addisoniidae and Cocculinellidae. This view has been accepted by PONDER & WARÉN (1988:310). Meanwhile, the anatomy of several lepetelloid families has been outlined in detail (HASZPRUNAR, 1987a, b, 1988a, b, c; McLEAN & HASZPRUNAR, 1987). Together with the detailed description of choristellid anatomy, which is presented here, the previous, preliminary conclusions will be substantiated or slightly modified based on the new data.

VERRILL (1882, 1884) first noted the peculiar feeding

biology of *Choristella*. As far as is known all species that have been found on a substrate live and feed in the empty egg cases of sharks (*e.g.*, *Scylorhinus*) or skates (*e.g.*, *Raja*) (see, *e.g.*, GUBBIOLI & NOFRONI, 1986). This mode of nourishment is shared solely with the lepetelloid limpet genus *Addisonia* (VILLA, 1985; RAGOZZI, 1985; McLEAN, 1985; HASZPRUNAR, 1987a). It will be shown that Addisoniidae and Choristellidae share not only a similar feeding biology, but also are closely related, despite the differences in their external morphology. This raises questions regarding the primitiveness of limpets such as Addisoniidae and all other cocculiniform families and coiled forms like the Choristellidae among the Cocculiniformia.

In the accompanying paper McLEAN (1992) provides a complete revision of the family including descriptions of certain new choristellid species and exclusions of taxa previously assigned to the family. Photographs of adult shells and SEM views of protoconchs, opercula, radulae, and jaws are presented there. Anatomical characters of certain species described by McLEAN (1992) are presented herein.

MATERIALS AND METHODS

Few specimens of each species were available for anatomical investigations and the preservation was poor in most cases. In addition, the content of the alimentary tract (see below) and an excessive amount of debris in the mantle cavity caused ruptures and folds in the sections. Nevertheless, I was able to reconstruct at least the gross anatomy

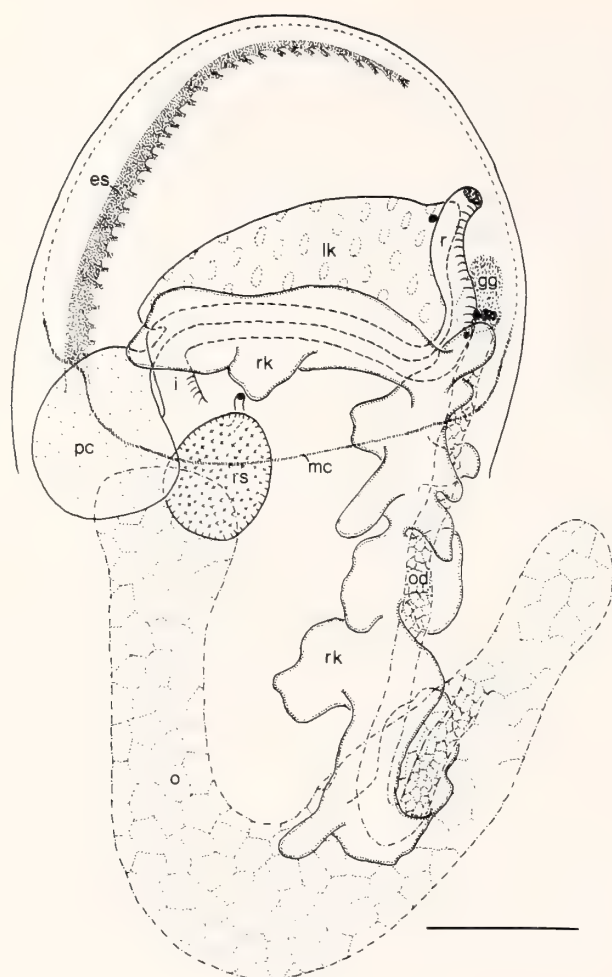


Figure 1

Choristella hickmanae, mantle cavity and gonopercardial system in dorsal view. Anatomy of the heart could not be determined in this species. Abbreviations: es, efferent gill sinus; gg, genital gland; i, intestine; lk, left kidney; mc, posterior end of mantle cavity; o, ovary; od, oviduct; pc, pericardium; r, rectum; rk, right kidney; rs, receptaculum seminis. Scale bar = 1 mm.

of the specimens, although uncertainties remain with respect to details of the nervous and circulatory system and of histology in general.

Abbreviations: LACM—Los Angeles County Museum of Natural History; NMNZ—National Museum of New Zealand, Wellington.

***Choristella marshalli* McLean, 1992:** Four males from the original type lot (NMNZ M.75210) have been investigated. The three adult specimens were embedded in paraplast and the 5- μ m serial sections (one series transverse, one oblique, one sagittal) were stained by Heidenhain's Azan method. A juvenile male was embedded in plastic (araldite) and the 2- μ m serial sections were stained by Regaud's fluid. According to Bruce A. Marshall (NMNZ;

personal communication) the specimens were frozen before preservation in alcohol; therefore, the preservation of external epithelia was poor.

***Choristella hickmanae* McLean, 1992:** A series of sections of a single female was available for anatomical investigation. According to McLean (personal communication) the live-collected specimen had been preserved in alcohol, resulting in a good preservation of all tissues. Thus, the histological description is mainly based on this specimen. The nearly transverse, 15- μ m-thick serial sections were stained by haematoxylin and eosin. Unfortunately, debris in the left side of the mantle cavity caused many folds in the sections and destroyed most of the cardiac region.

***Choristella nofronii* McLean, 1992:** This species was treated by GUBBIOLI & NOFRONI (1986) under the name "*Cithna naticiformis* Jeffreys, 1883," but the taxonomy was rectified by McLEAN (1992). A single juvenile female was available for serial sectioning. After being embedded in paraplast the specimen was sectioned in nearly transversal 5- μ m serial sections, which were stained by haematoxylin and eosin. It is probable that this specimen died before fixation, because the histological preservation of all tissues was poor.

Serial reconstruction was done by means of an ocular micrometer and millimeter paper (by "hand") as described in detail by HASZPRUNAR (1987a).

RESULTS

External Features

The head has a stout snout, and the oral lappets are weakly developed. Whereas the epithelium of the head consists of columnar cells, the region of the mouth opening is formed by tall columnar and cuticularized (true cuticula) cells (Figure 4). Cephalic lappets are lacking; the tentacles are devoid of papillae.

The mantle margin forms a simple fold lacking special glands or tentacles. Two thin blood sinuses and a mantle nerve supply the mantle border.

The epithelium of the pedal sole consists of tall, columnar, densely ciliated cells with elongated nuclei interspersed by very few mucous cells. Anteriorly a single, large pedal gland opens via a wide pore, which marks the border between the pro- and mesopodium. Laterally and posteriorly several smooth epipodial tentacles are present. The posterior dorsal surface of the foot bears an operculum (see also the accompanying paper of McLEAN, 1992). Many thin blood sinuses are found within the pedal musculature. In addition, a cell type containing many brownish droplets, the so-called "pore-cells," are interspersed (Figure 7). Similar cells are also present in the wall of the head and many occur in the mantle margin.

The single attachment zone and innervation (see HASZPRUNAR, 1985) indicate that there is a single (left) shell muscle, which has its origin on the columella of the shell.

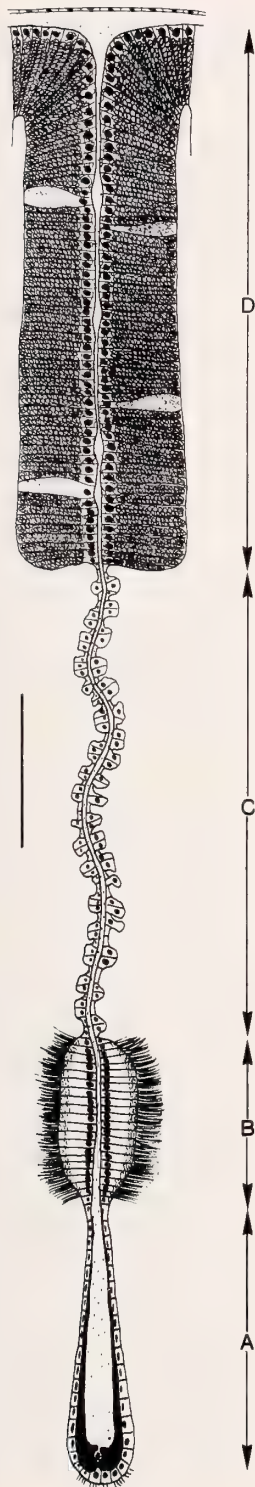


Figure 2

Choristella marshalli, sagittal section of a gill leaflet, anterior view, slightly schematized. A, B, C, D: zones of gill leaflet (see text). Scale bar = 100 μ m.

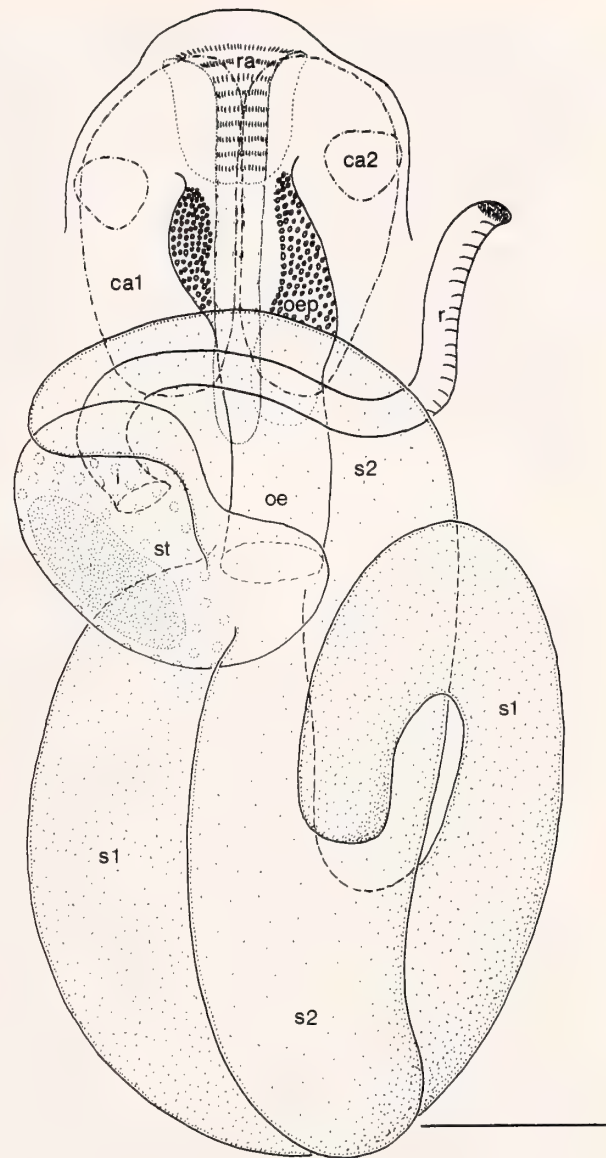
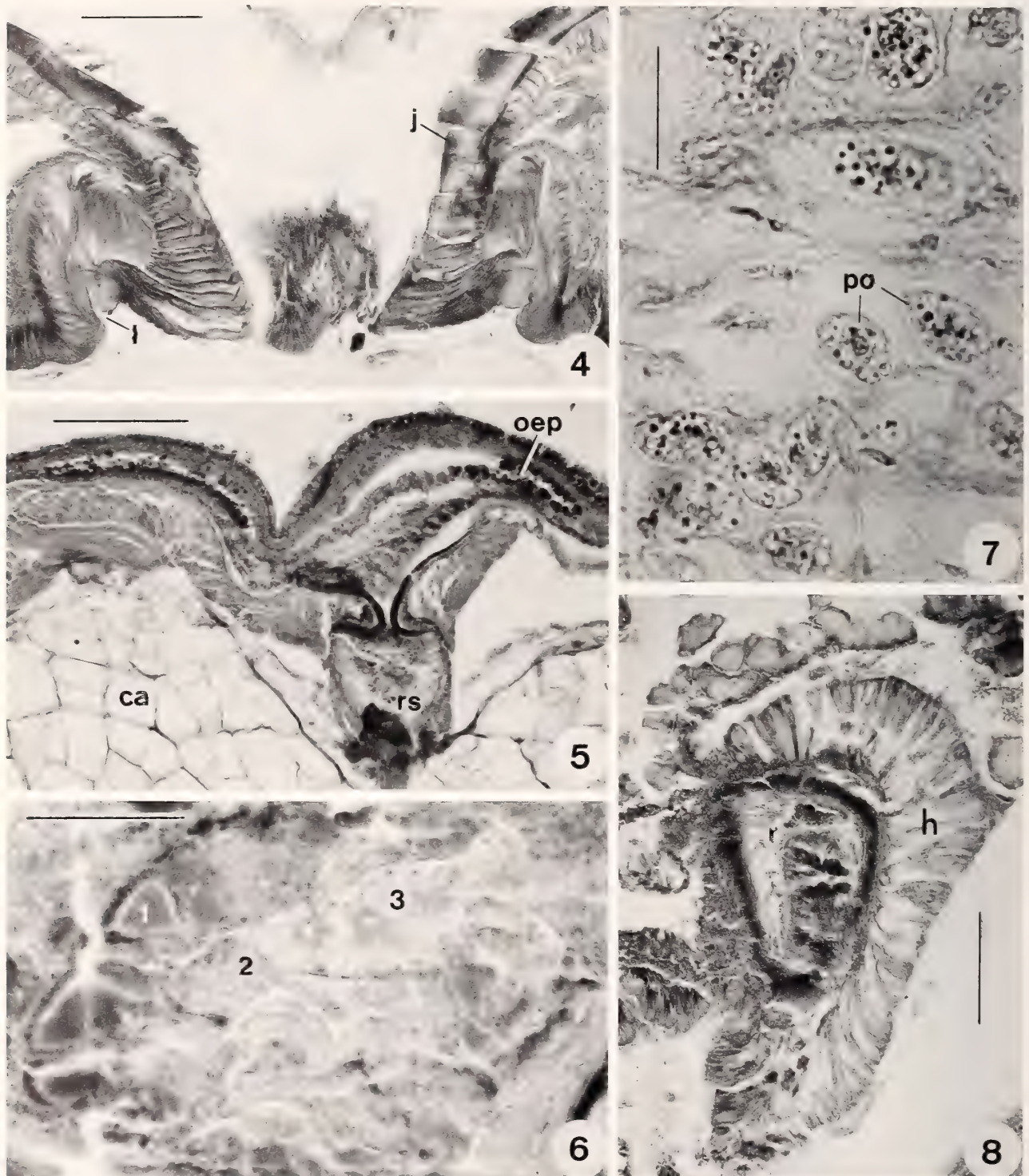


Figure 3

Choristella hickmanae, alimentary tract in dorsal view. Abbreviations: ca1, anterior radular cartilage; ca2, posterior radular cartilage; i, intestine; oe, posterior oesophagus; oep, oesophageal pouch; r, rectum; ra, radula; s1, left cul-de-sac; s2, right cul-de-sac; st, stomach with gastric shield. Scale bar = 1 mm.

Mantle Cavity

The mantle cavity is moderately deep. Numerous gill leaflets occupy most of the mantle roof, filling the space within the mantle cavity. Additional organs of the pallial roof include the single (left) osphradium to the very left, the anterior portion of the heart (to the left), and the left kidney (ventral). A branch of the right kidney is situated in the center, and a distinct portion of the intestinal sac lies dorsally. To the right of the mantle roof is the distal



Explanation of Figures 4 to 8

Figures 4–8. *Choristella hickmanae*, histological details. Figure 4. Jaws (j) and lips (l). Scale bar = 100 μ m. Figure 5. Radular cartilage (ca) and radular sheath (rs), and anterior oesophagus with asymmetrical oesophageal pouches (oep). Scale bar = 200 μ m. Figure 6. Oesophageal gland. 1, 2, 3 mark the various cell types (see text). Scale bar = 100 μ m. Figure 7. Pore cells (po) between muscle fibers and connective tissue (amorphous) in the foot mass. Scale bar = 20 μ m. Figure 8. Rectum (r) with typhlosole (t) near anus, underlain by hypobranchial(?) gland (h). Scale bar = 100 μ m.

portion of the rectum, which is underlain by a (hypo-branchial?) gland (Figure 8), and the genital opening, which is also surrounded by a gland (Figure 1).

As already noted by VERRILL (1882) the choristellid gill is pectinibranch and consists of numerous leaflets that have a highly characteristic structure (Figure 2): the efferent axis is stiffened by a pair of prominent, elongate skeletal elements, which emerge from the single skeletal rod of the gill axis. Distally the skeletal rods enclose a thin nerve that extends along to the efferent axis of the leaflet. More proximally they enclose the prominent efferent blood sinus. The epithelium at the efferent edge is cuboidal and sparsely ciliated. The following zone (A) is characterized by a squamous epithelium, which is still underlain by skeletal material. This is followed by a short region (B) forming a distinct band of columnar (up to 25 μm), densely ciliated cells with basally situated nuclei. The subsequent zone (C) is characterized by a non-ciliated epithelium, which appears folded because of different cell heights. Near the afferent axis the epithelium of the gill leaflet becomes abruptly much taller (up to 60 μm) and glandular (D). Two types of mucus cells are present, a rare one with a brightly stained amorphous interior, and one that is much more common and shows numerous dark-red stained granules that have concentric rings. The glandular zone of the leaflets occupies the entire dorsal mantle roof. The two juvenile specimens investigated lack the glandular zone of the gill leaflets.

To the right, the histology of the glandular zone of the gill changes successively and continuously in that only the bright mucus cells are present. This type of epithelium primarily underlies the rectum.

Heart, Circulatory and Excretory Systems

The pericardium is situated at the posterior end of the mantle cavity to the left. It is rather large with a single auricle situated anteriorly and to the left, and a ventricle which lies laterally to the left of the proximal portion of the rectum. After passing through one of the two kidneys, the blood is oxygenated either in the gill leaflets or (to a lesser extent) in the mantle edge. Both streams of blood, the ctenidial and the pallial ones, join at the entrance to the auricle. More peripheral pathways of the blood could not be reconstructed.

Two kidneys are present (Figure 1). The left one is large and is situated in the pallial roof. It has a simple opening immediately to the left of the anus. A broad, ciliated renopericardial duct is present. The opening of the right kidney is situated immediately to the right of the anus. The right kidney is composed of two large, elongated cavities. One occupies the mantle roof and extends to the left side; the other one extends posteriorly and surrounds the gonoduct (Figure 11). No connection with the pericardium could be found, and the histology of the renal epithelium differs considerably from that of the left kidney.

Genital System

There is no indication that choristellid species are hermaphroditic. All observed specimens of *Choristella marshalli* were males, whereas the single specimens of *C. hickmanae* and *C. nofronii* were females.

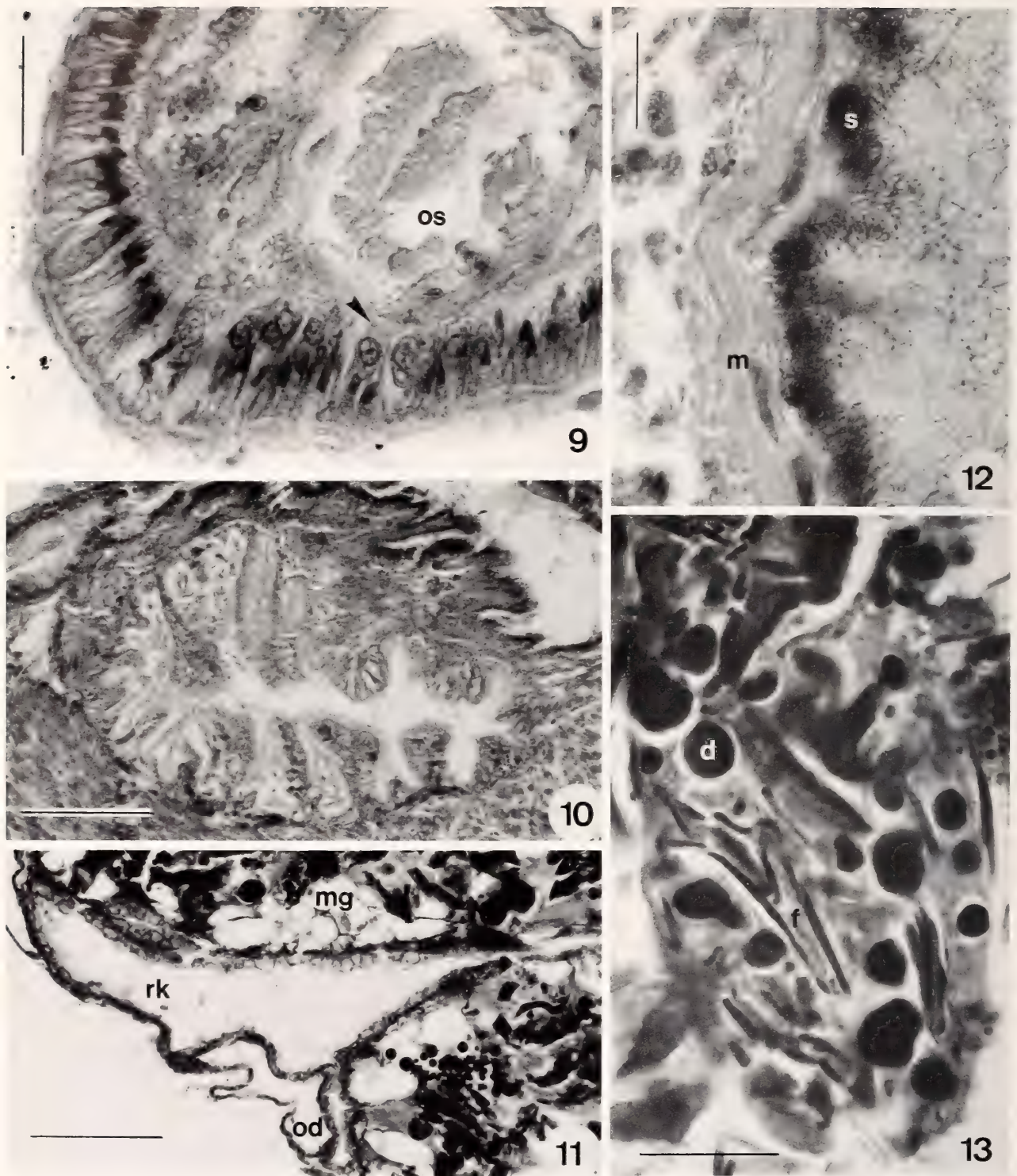
The ovary forms a compact mass and occupies the left dorsal portion of the visceral mass of the most apical whorl of the animal. It contains numerous yolk-rich eggs, which are provided with a distinct outer membrane. Eggs in all stages of development are present. There is no trace of any accessory gland for the formation of additional nutrients. The oviduct is a simple ciliated tube of somewhat irregular shape. It starts as a very wide tube, then narrows abruptly and extends forward, being situated at the very right side of the animal and adjacent to or embedded in the posterior lobe of the right kidney (Figure 11). The genital opening is located at the right posterior end of the mantle cavity. A large receptaculum (Figure 1: *rc*) is present, the anterior portion of which occupies the posterior pallial roof. The receptaculum is surrounded by a prominent muscular layer and is filled with sperm. The sperm cells are irregular in the center of the vesicle, whereas their heads are more or less oriented outwards near the wall (Figure 12). The receptaculum is provided with a short, narrow, muscular duct, which opens into the mantle cavity. There is no visible connection with the remaining genital system. The region anterior to the genital opening is characterized by a special glandular epithelium (Figure 1: *gg*) that is clearly distinct from the hypobranchial gland. The females lack an open seminal groove.

The testis consists of several lobes that cover the intestinal sacs dorsally and at the left side. Sperm cells in all stages of development are found within. Ripe sperm cells have elongated, spiral heads. The vas deferens forms a simple ciliated duct, which is filled with ripe sperm. Again there are no accessory glands. From the genital opening an open seminal groove extends forward along the right of the neck to the right cephalic tentacle, which is used for copulation. In contrast to females, a glandular area around the genital opening and a receptaculum are lacking.

Alimentary Tract

In *Choristella* the mouth opening of the alimentary tract (Figure 3) is provided with tall columnar (40 \times 3 μm) and cuticularized cells with elongated nuclei. Most of the anterior buccal cavity is cuticularized as well. The paired jaws are well developed and consist of numerous elements forming a honeycomblike structure (Figure 4; see also the accompanying paper by McLEAN, 1992). The sublingual pouch is reduced, and a subradular sense organ is lacking.

In general, the choristellid radula consists of 11 teeth per row and resembles that of *Cocculinella* (compare BUSH, 1897; THIELE, 1909; BOUCHET & WARÉN, 1979; HICKMAN, 1983; MARSHALL, 1983). For detailed descriptions of the radulae of the species investigated see the accom-



Explanation of Figures 9 to 13

Figures 9–13. *Choristella hickmanae*, histological details. Figure 9. Osphradial nerve (os) innervating sensory epithelium (arrowhead). Sensory cells have basal round nuclei; supporting cells are characterized by distal elongated nuclei. Scale bar = 20 μ m. Figure 10. Posterior oesophagus. Scale bar = 200 μ m. Figure 11. Midgut gland (mg), right kidney (rk), and oviduct (od). Scale bar = 200 μ m. Figure 12. Wall of receptaculum with circular muscle sheath (m) and sperm cells (s), which are densely arranged along the wall. Scale bar = 20 μ m. Figure 13. Huge midgut cell with large mucous droplets (d) and fibers from chondrichthyan egg cases (f). Scale bar = 100 μ m.

panying paper by McLEAN (1992). Two pairs of radular cartilages are present. The ventral pair is very large, consists of large cartilage cells (Figure 5), and is interconnected by a ventrally inserted horizontal muscle. The second pair is much smaller, consists of much smaller cells, and is positioned dorsally to the first pair (Figure 3). A thick oral sphincter could be observed; otherwise it was not possible to reconstruct the buccal musculature in detail.

The small salivary glands are situated dorsally and are simple glandular pouches without a distinct duct. Immediately posterior to their opening, the dorsal food channel begins with the appearance of two symmetrical, densely ciliated folds. The emergence point of the oesophagus is marked by the buccal commissure. The anterior oesophagus is quite simple and contains only the folds of the dorsal food channel. Laterally it conveys the products of the small oesophageal pouches, which produce very small dark-brown granules. In *Choristella marshalli* the pouches are of equal size, whereas in *C. hickmanae* the right one is about three times larger than the left (Figure 5). At this region the folds of the dorsal food channel flatten and disappear. The posterior oesophagus begins as a broad and simple duct of irregular shape without any folds. Its epithelium is ciliated and mucus cells are interspersed. After a short distance many large longitudinal folds arise abruptly and characterize the most posterior part of the oesophagus (Figure 10), which is provided with a specific gland.

This tubular gland surrounds the posterior oesophagus and is composed of three cell types (Figure 6): (1) Very small (diameter about 10 μm) cuboidal cells form the blind ends of the tubes and produce mucus that stains bright violet. The lumen of this region is wide (40 μm). (2) The epithelial cells of the proximal portion of each tube are much larger (diameter 25–30 μm), stain brightly and bear a microvillous border. The lumen is here very narrow, about 5 μm . (3) The cells of the distal region are of a similar size, contain reddish-staining material near their apical surfaces, and bear cilia. The lumen is here somewhat broader, about 10 μm . Numerous tubules enter the posterior oesophageal wall at its opening into the stomach.

The stomach region is highly modified and specialized. A prominent stomach is lined with ciliary tracts and contains a cuticular shield with a large tooth and a very small caecum. Mucus cells are interspersed in the epithelium of the stomach. Near the entrance of the oesophagus a large, densely ciliated fold separates two very large cul-de-sacs from the stomach region. The right sac is smaller, is situated more dorsally, and invades the posterior mantle roof. The left sac is situated ventrally and extends to the upper visceral whorls. The sacs contain large quantities of long pieces of the chondrichthyan egg cases that are in a mucoid matrix. The epithelium of the sacs consists of three distinct cell types: (1) Huge (diameter up to 400 μm) vacuolized cells, which are probably used for digestion, contain (phagocytosed?) food pieces (Figure 13). (2) Much smaller (maximum diameter 50 μm) mucus cells that stain violet.

(3) Mucus cells of the same size that contain many small, dark-brown granules. The last cell type is usually scattered among the others; it is the only type in a distinct area of the most anterior portion of the right sac.

The intestine is demarked from the ventral wall of the stomach by an abrupt change in diameter (from about 600 μm to 200 μm). The intestine is very short and is continued by the rectum (diagnosed by its position beneath and more distal to the heart) without a distinct change in histology. The rectum extends laterally to the heart, turns to the very right of the mantle roof, then runs forward and releases the feces into the mantle cavity via a simple anus. The rectum has a prominent typhlosole, whose cells are about three times higher than those of the remaining rectal epithelium (Figure 8).

Nervous System

The nervous system of all choristellid species investigated is uniform. It is wide, streptoneurous, and hypoathroid (*i.e.*, adjacent pleural and pedal ganglia).

The cerebral ganglia are situated laterally in the head and are interconnected by a long cerebral commissure. From the labial lobe the very thin buccal connectives emerge, leading to the buccal ganglia, which are situated to the left and right of the emergence point of the oesophagus. A thick but simple tentacular nerve is present; there are no traces of an optic nerve. In addition, the region of the mouth opening is supplied by several nerves.

The pleuro-pedal complex is the largest nervous center. Anteriorly situated pedal nerves supply the pedal gland and the anterior portion of the sole. Posteriorly the pedal ganglia give rise to long pedal cords, which are interconnected by several commissures. From the pedal cords fine side branches run to the epipodial tentacles.

The visceral chain starts with the pleural ganglia, which are located dorsal to the pedal ganglia. A thick pallial nerve emerges from each pleural ganglion and innervates the mantle border. The visceral chain is wide; the sub- and supraoesophageal ganglia are small. From the latter a connective nerve enters the mantle roof at the very left and swells to form an osphradial ganglion. The visceral (left) and genital (right) ganglia are distinct and are situated along the posterior end of the mantle cavity.

Sense Organs

Although an eye-lobe is present, there is no trace of eyes or optic nerves.

The osphradium is situated along the efferent gill axis. The epithelium is taller (about 20 μm) than the adjacent one (10–15 μm), lacks any zonation, and is primarily composed of two cell types (Figure 9): (1) Supporting cells with proximally situated, spindle-like, quite condensed nuclei and (2) sensory cells with basally situated, larger and round nuclei. The latter appear to have contact with the underlining osphradial ganglion because the basal lamina

is often interrupted. A very few large mucus cells are interspersed.

A subradular organ could not be detected.

The statocysts are situated posteriorly and adjacent to each other and abut the pedal ganglia, although they are supplied by a cerebral nerve, which is partly fused with the cerebropedal connective. The statocysts contain many small statoconia.

DISCUSSION

Character Analysis

Recently I have discussed the evolutionary history of the Cocculiniformia, including preliminary results on the Choristellidae (HASZPRUNAR, 1988c). Therefore the discussion below is restricted to the choristellid characters and to more controversial points of view.

Connective tissue of the foot: The cell type with many brownish droplets (Figure 7) calls for some comment. It does not form epithelia or compact mesenchymate tissues, but is always found interspersed, although sometimes in high densities. It occurs in the foot, the wall of the head, and in the mantle margin, in fact at all positions where massive connective tissue is present. Occurrence and cytology of this cell type are typical for so-called "pore-cells" ("Blasenzellen" by German authors such as WOLBURG-BUCHHOLZ, 1972), which have been described in a variety of gastropods and bivalves. In the latter group they have been called "brown cells." As reviewed by SIMKISS & MASON (1983) and MASON *et al.* (1984), the fine-structure (sievelike structure for ultrafiltration) of pore cells closely resembles that of podocytes, which however form epithelia. There is evidence that pore cells act in hemocyanin synthesis, in phagocytosis, in the recycling of respiratory pigments, or generally in metal ion metabolism. Among the streptoneuran gastropods, pore cells have been described in the connective tissue or blood sinuses from all parts of the body in *Littorina* (MARTOJA *et al.*, 1980; MASON *et al.*, 1984; BROUGH & WHITE, 1990), around the alimentary tract in *Rissoa* (MARTOJA & THIRIOT-QUIEVREUX, 1980), in the foot mass of *Diodora* sp. (Haszprunar, unpublished data), and in the osphradial connective tissue of *Campanile symbolicum* (HASZPRUNAR, 1992).

Gill: From the functional point of view the choristellid gill resembles a monopectinate ctenidium of caenogastropods or certain trochoids in serving for respiration as well as for water currents (*cf.* YONGE, 1947). However, the choristellid gill leaflet has two regions where gas exchange could occur, distally (efferent) and proximally (afferent) of the ciliary band, whereas a monopectinate ctenidium has the proximal zone alone. Also the afferent glandular zone is a peculiarity of the choristellid gill that contrasts with the typical monopectinate ctenidium.

The choristellid gill resembles closely that of the Addisoniidae (*cf.* HASZPRUNAR, 1987a). Both gill types are

monopectinate, spread over the whole mantle roof, and share the presence of paired skeletal support of the leaflets as well as a highly glandular epithelium composing the large proximal portion. Differences occur in that the choristellid gill leaflets have a distinct ciliary band, whereas in addisoniids the ciliary cells are spread over the whole surface of the distal leaflets. Nevertheless, the addisoniid and choristellid gills are very similar in shape and structure and are probably homologous. It has been argued (HASZPRUNAR, 1987a) that the addisoniid gill may also function in brooding, because of the lack of the glandular zone in juveniles. Juvenile choristellids also lack the glandular zone; however, the glandular zone is well developed in males, contradicting the brooding hypothesis at least in the Choristellidae.

The complete lack of the glandular zone in juveniles also contradicts an interpretation of the rectal portion of this gland as a hypobranchial gland. A hypobranchial gland would be expected to be present in juveniles as well as in adults.

Judging from the characteristics of the gill in the more primitive lepetelloid families, I have argued against the ctenidial nature of lepetelloid gills (HASZPRUNAR, 1988c, d). On the other hand, the choristellid gill fits nearly all characters typical for gastropod ctenidia, including the presence of skeletal rods, the presence of a distinct ciliary band and a distinct respiratory zone, innervation, and blood supply. In addition, the presence of specific sensory pockets (bursicles) in the gill leaflets of several lepetelloid families (Lepetellidae, Pseudococculinidae, Pyropeltidae, Bathyphytophilidae), which are likewise present at the ctenidial leaflets of vetigastropods (*e.g.*, SZAL, 1971; HASZPRUNAR, 1987b), calls for homology. Although I still think that a non-ctenidial nature of the lepetelloid, and thus of the choristellid gill, is more probable than the opposite assumption (modified ctenidia), ontogenetic data are needed to confirm this view more convincingly.

Circulatory and excretory system: The general organization of the choristellid circulatory and excretory systems is very similar to that of lepetelloids. In particular, the separation of the right kidney from the pericardium, as well as from the genital system, is shared with several lepetelloid families such as Osteopeltidae, Cocculinellidae, and Addisoniidae (HASZPRUNAR, 1987a, 1988a, c; see Table 3). Outside the Cocculiniformia this condition is found also in the Seguenziidae (HASZPRUNAR, 1988d:fig. 2Q).

Genital system: The Choristellidae are unique among the Cocculiniformia (Lepetelloidea) in being gonochoristic. As outlined elsewhere (MCLEAN & HASZPRUNAR, 1987; HASZPRUNAR, 1988c; Table 2), Lepetelloidea show a trend from hermaphroditism to gonochorism, and the Choristellidae appear to represent the final step of this trend. Such a postulated trend (in contrast to the opposite direction) largely parallels the increasing specialization of the alimentary tract (see below) and is further supported by

the hermaphroditic condition in the sister group Cocculinioidea (outgroup comparison). The logical conclusion is that the choristellid gonochorism probably is a secondary phenomenon. Similar trends from hermaphroditism to gonochorism exist in various bivalve subgroups (MACKIE, 1984), and reproductive strategy may vary even within molluscan genera; therefore, the choristellid (lepetelloid) situation is not exceptional.

Among the Lepetelloidea, a separated receptaculum with an opening in the center (slightly left) of the posterior mantle roof is present only in Addisoniidae and Choristellidae. However, a similar arrangement exists in the archaeogastropod *Melanodrymia aurantiaca* (see HASZPRUNAR, 1989), in the seguenziid *Carenzia carinata* (Haszprunar, unpublished data), and in skeneid-like archaeogastropods living on sunken wood such as *Leptogyra constricta* or *Xyloskenea costulifera* (see MARSHALL, 1988; Haszprunar, unpublished data). Thus, convergence cannot be excluded. Because the more primitive lepetelloid families do not have true receptacula, the addisoniid-choristellid receptaculum is unlikely a plesiomorphy of the Lepetelloidea.

Like the remaining Lepetelloidea the Choristellidae use the more or less modified right cephalic tentacle for copulation. The Bathysciadiidae in contrast always have a distinct copulatory organ (THIELE, 1908; HASZPRUNAR, 1988c), whereas both states are present in different genera of the Cocculinidae (HASZPRUNAR, 1987c).

Alimentary tract: The choristellid jaws are unique for the superfamily and constitute an apomorphy of the family (MCLEAN, 1992). The choristellid jaws can be easily derived from the teethlike jaw-elements present in other cocculiniform families such as Pseudococculinidae, Pyropeltidae, and Osteopeltidae (HASZPRUNAR, 1988c). In general, modification (Choristellidae), reduction (Cocculinidae), or even loss of jaws (Lepetellidae, Bathyphytophilidae, Cocculinellidae, Addisoniidae) is common among the Cocculiniformia.

Whereas the presence of two radular cartilages is common among primitive Gastropoda (HASZPRUNAR, 1988d), the dorsal position of the posterior cartilage appears unique for the Choristellidae.

The similarity of the choristellid and cocculinellid radula has been mentioned by HICKMAN (1983) and is confirmed by MCLEAN (1992). However, it is possible that this type has evolved independently in the Cocculinellidae and Choristellidae. Again, radular modifications are common among the Cocculiniformia.

The choristellid midgut region is difficult to interpret, and in particular the region of the entrance of the oesophagus into the stomach offers problems. Here the "circumoesophageal" tubules and the two cul-de-sacs release their products into the alimentary tract. One may regard the "circumoesophageal" tubules as a fused and modified midgut gland, which is possible from the positions of their

openings. In this case, the homology of the cul-de-sacs would become questionable, because cul-de-sacs as a specialized portion of a stomach are not known among the Archaeogastropoda.

The second possibility, which is much more likely in my view, is that the cul-de-sacs represent (paired) aberrant midgut glands. Indeed, the position of the respective openings correspond exactly with those of typical midgut glands. In addition, a pallially situated portion of the right midgut gland is also present in the Cocculinellidae (HASZPRUNAR, 1988a). The argument that a molluscan midgut gland does not contain food particles is contradicted by conditions of the Lepetellidae and Bathyphytophilidae, where such midgut glands are present (Haszprunar, unpublished data).

However, under this assumption the homology of the "circumoesophageal" glands becomes obscure, since there is no equivalent for this structure in other gastropods. The position of the openings (close to the entrance point into the stomach) and the presence of true oesophageal pouches indicate that they are not true oesophageal glands. However, recent investigations on a new species of *Bathyphytophilus* (Haszprunar, unpublished data) also revealed peculiar outpockets of the posterior oesophagus, which possibly serve as a reservoir for symbiotic bacteria. Despite the quite different histology, the choristellid circumoesophageal gland might have a similar function.

The topic becomes more complicated when the choristellids are compared with the remaining lepetelloid families, in particular with the Addisoniidae (identical nourishment and similar gill type, see above). There the stomach is lost and the distal intestine forms a wide saclike tube (HASZPRUNAR, 1987a, 1988a). Although the respective midgut glands are somewhat specialized, there are no food particles within. In any interpretation these conditions contrast with those of the Choristellidae, where certainly non-intestinal (position of openings) cul-de-sacs store the mass of food particles and a "circumoesophageal gland" is present.

These differences also lead to the question of whether the use of a common food source in the Choristellidae and Addisoniidae is due to convergence or due to a common ancestor (see below). Among the Cocculiniformia in general a common food source does not necessarily parallel the organization of the alimentary tract: (1) The cocculinid genus *Teuthirostria* (known from its radula) and Bathysciadiidae feed on cephalopod beaks, yet their radulae are entirely different. (2) Osteopeltidae and Cocculinellidae live on bone (but see below), yet the anatomies of the guts are very different. In all cases this may be because of different strategies in nourishment: although food (bone, egg cases, etc.) are usually found in high density in the alimentary systems, nourishment might be either on the decaying bacteria of the respective substrate or on the substrate itself by specific enzymes or with the aid of symbiotic bacteria. Studies of the ultrastructure of the gut contents are necessary to clear up this point.

No conclusion about the specific mode of nourishment of the Choristellidae can be reached at the present. Judging from the sections, phagocytosis appears probable, but symbiosis with bacteria cannot be excluded. It is also not known whether bacterial and/or fungal activity is necessary before the nutrients are available for the animals.

Nervous system and sense organs: The choristellid nervous system does not show any peculiarities; the hypoathroid condition once more reflects the archaeogastropod nature of the family.

Absence of eyes is a common phenomenon among deep-sea gastropods and is thus of minor phylogenetic significance. Lepetelloidea always have statocysts with several statoconia (HASZPRUNAR, 1988c). On the other hand, statoconia are present in various archaeogastropod groups such as the Patellogastropoda (Docoglossa), Vetigastropoda, and Seguenziidae, and are therefore of minor phylogenetic importance.

Phylogenetic Position of the Choristellidae

Internal classification: As already noted by McLEAN (1992), our studies are hampered by the lack of available specimens with soft parts. This also makes it impossible to give clear anatomical support for the species diagnoses presented by McLEAN (1992). Most probably, characters of the copulatory organ will be useful to distinguish species and possibly also genera as in other lepetelloid families (e.g., Pseudococculinidae; see HASZPRUNAR, 1988b), although this cannot be verified at present, because males were available of *Choristella marshalli* only.

Lepetelloid affinities: The lack of a larval shell (i.e., shell produced by the mantle margin prior to metamorphosis), the streptoneurous and hypoathroid central nervous system with pedal cords, the presence of two kidneys, and the type of anterior oesophagus with oesophageal pouches leave little doubt that the Choristellidae belong to the Archaeogastropoda (sensu HASZPRUNAR, 1988c, d). Apart from the shell (see below) all remaining choristellid characters fall well within cocculiniform and lepetelloid variability; not a single character contradicts this view. In particular the coelomic conditions (two kidneys and a separated, non-glandular gonoduct), the cocculinellid-like radula (MOSKALEV, 1978; HICKMAN, 1983) and the addisoniid-like gill and nourishment favor an inclusion of the Choristellidae in the Lepetelloidea. In addition, cocculiniform groups are well known to be specialized on various aberrant food in the deep sea (HICKMAN, 1983; MARSHALL, 1986; HASZPRUNAR, 1988c).

Relationships to lepetelloid families: HASZPRUNAR (1988c, submitted in 1986) based his conclusions about choristellid affinities on preliminary investigations. In the light of this much more detailed study on choristellid anatomy, some modifications to the original hypothesis on choristellid relationships are necessary. In particular, it is not possible to derive the choristellid alimentary system with

its well-developed stomach from the cocculinellid (reduced stomach) or addisoniid (lost stomach) condition as assumed originally.

A cladistic analysis using the software program Hennig'86 (FARRIS, 1988) was made to infer the phylogenetic relationships of the Choristellidae among the Lepetelloidea. Table 1 provides information concerning character states and the taxa of all higher lepetelloid families. From these, the characters of heart, conditions of kidneys, genital system, and cerebropedal ring have not been considered in the analysis, because they do not provide useful information on the topic (no differences or autapomorphies). All families are considered to be monophyletic, which is strongly indicated by their diagnostic radular type; all characters were given equal weight. The Pseudococculinidae and/or Osteopeltidae were taken as outgroups, with the same result.

To infer relationships, estimations of the probability of homology prior to cladistic analysis are necessary. The following basic assumptions were made: (1) Because of their detailed similarity and high complexity I regard as homologous the gills of Addisoniidae and Choristellidae (monopectinate, skeletal rods, distinct proximal glandular zone). (2) Also considered homologous are the distinct modifications of the alimentary tracts of Cocculinellidae and Addisoniidae (stomach reduction or loss, large granules in digestive gland and intestinal sac). (3) In contrast, the identical food source of Addisoniidae and Choristellidae cannot be unequivocally interpreted (see above). (4) According to the arrangement of teeth, a derivation of the addisoniid radular type from the cocculinellid-choristellid one appears possible (MARSHALL, 1987). (5) The cocculinellid gill is known in detail for *Cocculinella minutissima* (Smith) alone, where it is reduced to two vestigial knobs (HASZPRUNAR, 1988a). However, personal observations on several total specimens of *Cocculinella osteophila* Marshall (see Acknowledgments) revealed a more prominent pallial gill consisting of several leaflets like those of most lepetelloid families. Unfortunately the preservation was too poor to study the histology of this gill. Outgroup comparison suggests a reduction of the gill in *Cocculinella minutissima*; the basic cocculinellid gill probably resembles the pseudococculinid-osteopeltid condition. (6) Bone feeding of osteopeltids (what bone; cf. MARSHALL, 1987; WARÉN, 1989) and cocculinellids (fish bone; cf. MARSHALL, 1983; HASZPRUNAR, 1988a) is considered analogous: the habitat and fauna of large decomposing whales resemble those of the sulfide-rich seeps and vents (SMITH *et al.*, 1989), in contrast to those of smaller decomposing fish. Indeed, there might be an ecological link between the whale-bone feeding Osteopeltidae and the hot-vent living Pyropeltidae (a new species of which has been found recently also on whale bone; McLean, personal communication); both families exhibit radula of the pseudococculinid-like type. In addition, the alimentary tracts of Osteopeltidae and Cocculinellidae differ largely, and distinct similarities between both families are lacking.

Table 1

Comparative data on Osteopeltidae, Cocculinellidae, Choristellidae, Addisoniidae, and Pseudococculinidae. 0 = plesiomorphic; 1, 2, 3 = apomorphic; U = unordered.

Character	Family				
	Osteopeltidae	Cocculinellidae	Choristellidae	Addisoniidae	Pseudo-cocculinidae
Shell	symmetrical limpet (0)	symmetrical limpet (0)	coiled (2)	asymmetrical limpets (1)	symmetrical limpet (0)
Oral lappets	lacking (1)	lacking (1)	present (0)	lacking (1)	present (0)
Epipodium (U)	one pair (0)	none (1)	many pairs (2)	none (1)	one pair (0)
Gill	prominent (0)	prominent/vestigial(?)*	well developed (0)	well developed (0)	well developed (0)
Leaflets	lacking skeletal rods (0)	—(?)*	with skeletal rods (1)	with skeletal rods (1)	no skeletal rods (0)
	no special zonation (0)	—(?)*	with proximal gland (1)	with proximal gland (1)	no proximal gland (0)
Heart	monotocardian (0)	monotocardian (0)	monotocardian (0)	monotocardian (0)	monotocardian (0)
Kidneys	two, different (0)	two, different (0)	two, different (0)	two, different (0)	two, different (0)
Genital system	hermaphroditic (0)	hermaphroditic (0)	gonochoristic (1)	hermaphroditic (0)	hermaphroditic (0)
Gonoduct(s)	separated (1)	separated (1)	separated (1)	separated (1)	fused (0)
Separated receptaculum	not present (0)	not present (0)	present (1)	present (1)	not present (0)
Jaws	present (0)	lacking (1)	present (0)	lacking (1)	present (0)
Radula (U)	rhypidoglossate (0)	cocculinellid-type (1)	cocculinellid-like (1)	addisoniid-type (2)	rhypidoglossate (0)
Anterior oesophagus	glands (1)	glands (1)	pouches (0)	glands (1)	pouches (0)
Stomach (U)	prominent (0)	reduced in size (1)	prominent (0)	lost (2)	prominent (0)
Midgut gland (U)	normally structured (0)	large granules (1)	extremely modified (2)	large granules (1)	normally structured (0)
Intestine (U)	long, narrow (0)	long, 1st loop widened (1)	short, narrow (2)	long, 1st loop widened (1)	long, narrow (0)
Rectum	through heart (0)	through heart (0)	passes heart (1)	passes heart (1)	through heart (0)
Feeding on (U)	whale bone (1)	fish bone (2)	shark/skate egg cases (3)	shark/skate egg cases (3)	wood/algal holdfasts (0)
Cerebropedal ring	somewhat concentrated (1)	wide (0)	wide (0)	wide (0)	wide (0)
Pedal cords	present (0)	pedal nerves (1)	present (0)	present (0)	present (0)
Eyes	with pigment (0)	present/lost(?)†	lost (1)	lost (1)	present/lost(?)

* *Cocculinella minutissima* has vestigial gill leaflets (HASZPRUNAR, 1988a), whereas *C. osteophila* has several prominent gill leaflets of unknown structure (personal observations).

† *Cocculinella minutissima* lacks eyes (HASZPRUNAR, 1988a); *C. osteophila* lives in very shallow water (about 13 m depth, MARSHALL, 1983) and probably has eyes.

A single most parsimonious tree (28 steps, $ci = 89$, $ri = 75$) was created with a sequential arrangement of taxa: Pseudococculinidae, Osteopeltidae, Cocculinellidae, Choristellidae, and Addisoniidae. Of course this result depends heavily on the input matrix and on the basic assumption that changes of all characters are of the same likelihood. The result might be different if the remaining lepetelloid families, Lepetellidae and Bathyphytophilidae, the detailed anatomy of which remains to be outlined (Haszprunar, in preparation), are included in the analysis. Therefore I regard it as a provisional arrangement.

Concerning classification I still prefer a sequential arrangement of lepetelloid families without the naming of any node in the tree (*cf.* HASZPRUNAR, 1988c).

Shell shape and related characters: Among the Cocculiniformia, choristellid species are unique in having a coiled teleoconch, and among the Lepetelloidea they are the first example known to be lacking the otherwise typical condition that the protoconch tip is partially immersed in the posterior slope of the teleoconch ("fused protoconch tip" of MARSHALL, 1986). Generally it is accepted that gastropod limpets are *always* derived from coiled forms (*e.g.*, YONGE, 1947; FRETTER & GRAHAM, 1962; MCLEAN, 1981); if so, the Choristellidae should represent the most primitive condition among the Cocculiniformia respectively among the Lepetelloidea. However, this is in direct contrast to the sequence obtained by the cladistic analysis (see above).

According to this and previous phylogenetic analyses (HASZPRUNAR, 1988c; here) the assumption of primitive coiled teleoconchs in the Cocculiniformia would imply the postulation of parallel evolution of limpets, at least twice among the Cocculiniformia: once in the Cocculinoidea (Cocculinidae and Bathysciadiidae) and a second time in the Lepetelloidea (Lepetellidae, Pseudococculinidae, Bathyphytophilidae, Pyropeltidae, Osteopeltidae, Cocculinellidae, and Addisoniidae). If the Addisoniidae are accepted as a sister-group of the Choristellidae, the addisoniid condition forces the assumption of another event to evolve limpets. If the sequence revealed by the cladistic analysis above is accepted, even further events of evolution of a limpet shell are to be assumed. Admittedly, the evolution of limpets has often occurred among the Archaeogastropoda. However, in most cases the assumption of the derived nature of the limpet shell form can be substantiated by a more or less coiled juvenile teleoconch. In contrast, there is no trace of juvenile coiling of the teleoconch in any species of the remaining cocculiniform families. This is also the case in all Patellogastropoda (Docoglossa), which are now regarded as the most primitive gastropod group (WINGSTRAND, 1985; LINDBERG, 1988a, b; HASZPRUNAR, 1988c, d). As outlined in detail elsewhere (HASZPRUNAR, 1988c, d), I consider the uncoiled limpet form to be primary and coiled forms secondary in early gastropod evolution. I frankly admit that this hypothesis needs further confirmation to be generally accepted. In particular, details of the torsion process of patellogastropods and cocculiniforms

should be comparatively reinvestigated by the application of modern techniques (staining methods, video, *etc.*) to progress with this topic. Nevertheless, also in the light of the new data on Choristellidae and the result of the cladistic analysis above, I think it justified to consider the present dogma of primary coiled forms in the Gastropoda at least with some hesitation and to keep the alternative in mind.

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The Fine Structure of the Columellar Muscle of Some Gastropod Mollusks

by

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Abstract. The ultrastructure of the columellar muscle of five species of prosobranch gastropod with a conical spiral shell, one species (*Haliotis spadicea*) with a dome-shaped spiral shell, and two pulmonates (*Siphonaria capensis* and *S. concinna*) with a conical limpet shell is described. All species have muscle cells (designated Type I) which contain the conventional contractile apparatus of randomly arranged thick and thin filaments, few dense bodies and mitochondria, and a poorly developed sarcoplasmic reticulum. When measured from sections of tissue, the thick filaments range in mean diameter from 26 nm in *Turbo sarmaticus* to 69 nm in *Burnupena cincta*. Thick filament diameters measured from preparations of isolated filaments are always larger, ranging from 34 nm in *T. sarmaticus* to 83 nm in *Siphonaria* spp. The diameters of the muscle cells and the thick filaments within the cells of spiral-shelled gastropods are, with the exception of the sandy beach whelk *Bullia rhodostoma*, smaller, when compared to those in the columellar muscle of limpets. All thick filaments have an axial periodicity (about 14 nm) or Bear-Selby net, a feature of filaments that contain paramyosin. A second type of muscle cell (Type II), in the columellar muscle of *Burnupena cincta* and *Bullia rhodostoma*, is described. These cells contain bundles of thin filaments which are striated in appearance (periodicity range, 92 to 104 nm). Associated with the muscle is collagenous connective tissue. Whereas the muscle cells of the columellar muscle from *H. spadicea* and *Siphonaria* spp. are surrounded by collagen only, those of gastropods with spiral shells are often separated by vesicular spaces, thought to be blood spaces.

INTRODUCTION

The pedal musculature of gastropods is composed of two distinct regions, the columellar muscle and the tarsic muscle, that differ structurally and functionally (VOLTZOW, 1988, 1990; FRESCURA & HODGSON, 1990). The columellar muscle arises in the foot and is inserted onto the columella of the shell. In gastropods with a spiral shell, the principal functions of this muscle are to extend and retract the head and foot into or out of the shell and to rotate the foot (FRETTER & GRAHAM, 1962; BROWN & TRUEMAN, 1982; TRUEMAN & BROWN, 1985; TRUEMAN & HODGSON, 1990). These actions may result in considerable changes in the length of the columellar muscle. By contrast, in gastropods with a conical shell (limpets), the principal function of the columellar muscle is to raise the shell off or clamp it firmly against the substratum. Clamping is achieved by powerful contractions of the columellar muscle with minimal change in muscle length (FRESCURA, 1991). The differing functions of the columellar muscle of

gastropods with different shell forms suggest that structural differences might exist that would reflect the different roles of the muscle.

The structure and arrangement of muscle bundles or fibres within the columellar muscle have been described in detail at the light microscope level for a range of gastropods (ROTARIDES, 1941; TRUEMAN & BROWN, 1976, 1985; GAINES, 1976; BROWN & TRUEMAN, 1982; VOLTZOW, 1990; TRUEMAN & HODGSON, 1990; FRESCURA & HODGSON, 1989, 1990). Rather less is known of the fine structure of the columellar muscle. The only studies to date appear to be by PLESCH (1977) on *Lymnaea stagnalis*, HUDDART *et al.* (1977) on *Buccinum undatum* and *Neptunia antiqua*, WATABE *et al.* (1986) on *Batillus cornutus*, and FRESCURA & HODGSON (1989, 1990) on patellid limpets.

The aims of this study are to examine the fine structure of the columellar muscle of prosobranch gastropods that have spiral shells, and compare the findings with our previous work on prosobranch limpets (FRESCURA &

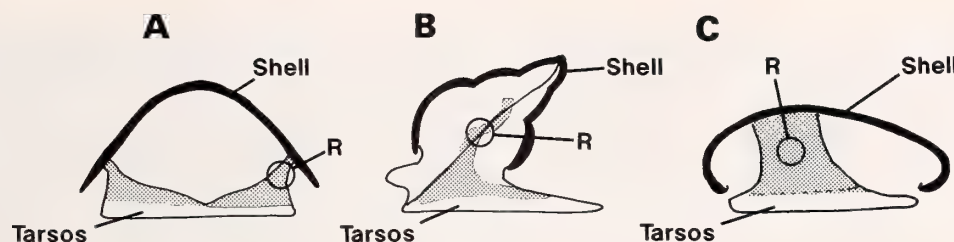


Figure 1

Schematic diagrams to illustrate the regions (R) from which columellar muscle was sampled from the limpets (A), gastropods with spiral shells (B), and *Haliotis* (C).

HODGSON, 1989, 1990). In addition we present findings on the structure of the columellar muscle of the pulmonate limpet *Siphonaria*.

MATERIALS AND METHODS

Eight species of gastropod with different shell forms were collected from rocky and sandy shores of the east coast of South Africa. Gastropods inhabiting the rocky shores included four species (*Burnupena cincta* (Röding, 1798), Buccinidae; *Oxystele sinensis* (Gmelin, 1791) and *O. tigrina* (Anton, 1839), Trochidae; *Turbo sarmaticus* Linné, 1758, Turbinidae) with shells that were spiral and conical, one species (*Haliotis spadicea* Donovan, 1808, Haliotidae) with a spiral but dome-shaped shell, and two species (*Siphonaria capensis* Quoy & Gaimard, 1833, and *S. concinna* Sowerby, 1824; Pulmonata) with a limpet form of shell. One species (*Bullia rhodostoma* Reeve, 1847, Nassariidae) with a spiral, conical shell was collected from the intertidal zone of a sandy beach. Animals were transported to the laboratory and housed in seawater aquaria until dissected, usually within 24 hr of collection.

For light microscopy, portions of the mid-regions of the columellar muscle (Figure 1) were fixed in either 5% formal saline or Bouin's aqueous fixative, embedded in Paraplast, sectioned at 6 μ m and stained by two methods: Milligan's trichrome, omitting orange G stain, and Mallory's trichrome (HUMASON, 1967). Both methods differentiate between collagenous connective tissue and muscle.

For electron microscopy, pieces of tissue about 1 mm³ were excised from the mid-region of the columellar tissue (Figure 1) under seawater and fixed in 2.5% glutaraldehyde in seawater (approximately isosmotic with tissues) for 12 hr at 4°C. Fixed tissue was washed in 0.1 M sodium cacodylate buffer (pH 7.2), postfixed with 1% osmium tetroxide in the same buffer for 90 minutes, dehydrated, and embedded via propylene oxide in an Araldite CY212/Taab 812 resin mixture (CROSS, 1989). Silver/gold sections, cut using glass knives, were stained either with 5% aqueous uranyl acetate for 30 minutes, followed by lead citrate for 10 minutes, or with 10% methanolic uranyl acetate for 30 minutes. Material was viewed on a Jeol JEM CXII electron microscope at 80 kV.

Isolated filaments were also prepared for transmission

electron microscopy from the columellar muscle of *Burnupena cincta*, *Oxystele sinensis*, *Turbo sarmaticus*, *Bullia rhodostoma*, *Haliotis spadicea*, and *Siphonaria concinna*. For comparison, isolated filament preparations were made from four species of patellid limpet (*Patella granularis*, *P. oculus*, *P. cochlear*, and *P. tabularis*), the fine structure of the columellar muscle from these limpets having been described in a previous paper (FRESCURA & HODGSON, 1990). For all species, filaments from the dorsoventral bundles of the columellar muscle were homogenized using a Sorvall blender. All mechanical parts and tissue were kept at 0°C. To remove soluble proteins, tissue was transferred to a buffer containing solutions with the final concentrations of 60 mM KCl, 5 mM MgCl₂, 1 mM NaN₃, 0.5 mM EGTA, 10 mM Imidazole, 5 mM DTT, 0.5% Triton X-100, 2 μ g/mL leupeptin, pH 7.0 at 4°C. Tissue was washed and spun again before being incubated in a medium containing solutions of a final concentration of 80 mM KCl, 5 mM MgCl₂, 2 mM NaN₃, 5 mM EGTA, 10 mM ATP, 20 mM MES-KOH, 5 mM DTT, 2 μ g/mL leupeptin, pH 6.0 at 4°C for 30 minutes on ice to dissociate the thick and thin filaments. Isolated filaments were negatively stained with 10% methanolic uranyl acetate on carbon or formvar coated copper grids and viewed using a Jeol JEM CXII transmission electron microscope at 80 or 100 kV. All chemicals were obtained from Sigma Chemical Company, USA.

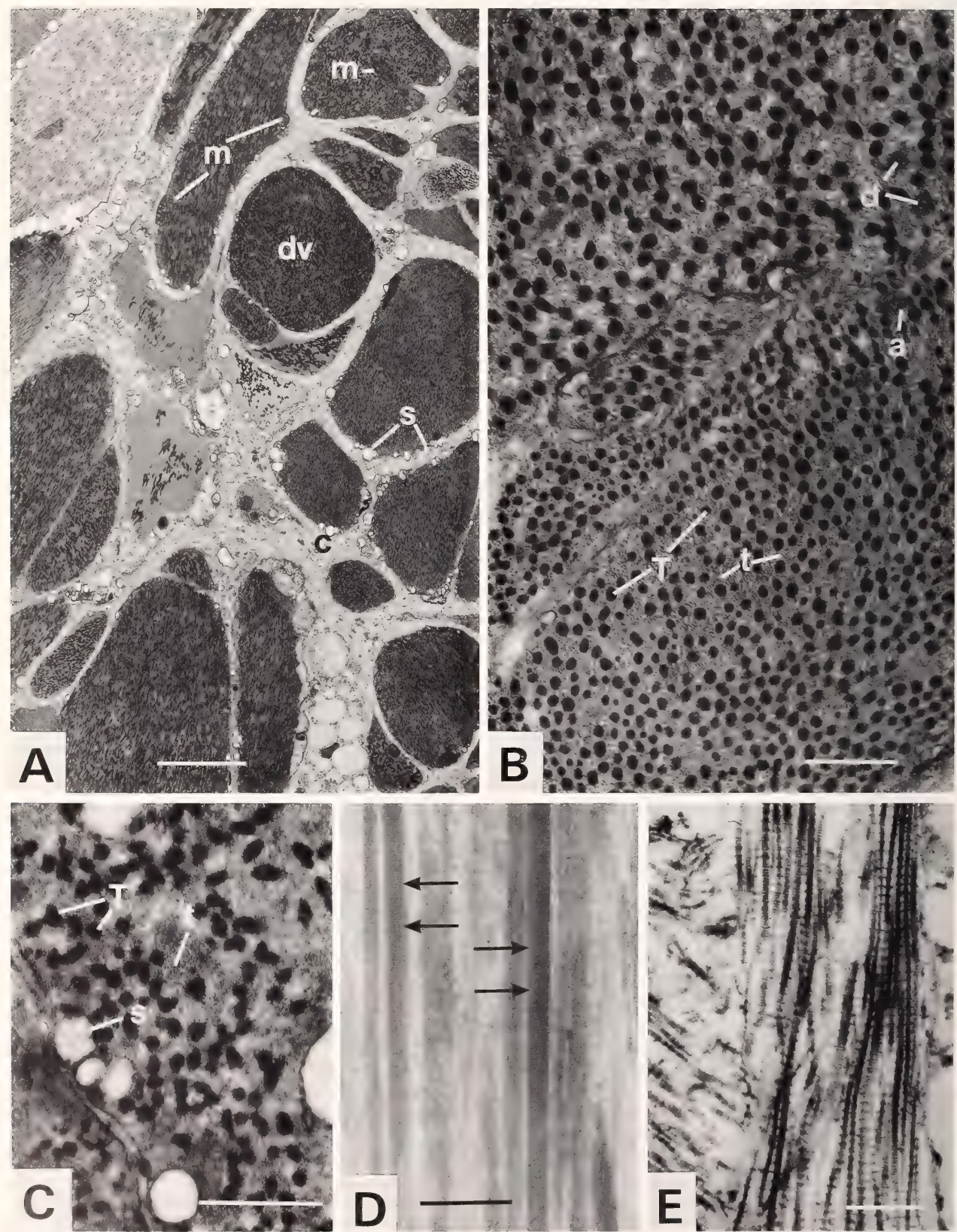
All measurements presented in the results were taken from photographs using a Summagraphics digitizing tablet and SigmaScan (Jandel Scientific, USA) software.

RESULTS

Organization of the Columellar Musculature

Light microscopy revealed that the arrangement of muscle within the columellar muscle of all species is similar to that previously described for other gastropods (ROTARIDES, 1941; TRUAMAN & BROWN, 1976, 1985; GAINES, 1976; BROWN & TRUAMAN, 1982; VOLTZOW, 1990; TRUAMAN & HODGSON, 1990; FRESCURA & HODGSON, 1990). Therefore only a brief description follows.

The majority of muscle fibres are orientated along the long axis of the columellar muscle. These muscle fibres



are divided into bundles by transverse and oblique muscles. In most species the longitudinal muscle bundles can be up to 150 μm in diameter. The muscle is surrounded by collagenous connective tissue, which occupies all of the intercellular space in *Siphonaria* spp. and *Haliotis spadicea*, and most of the intercellular space in *Turbo sarmaticus*, *Burnupena cincta*, *Bullia rhodostoma*, and *Oxystele* spp. In the latter case some small intercellular spaces were observed. As reported in a previous paper (FRESCURA & HODGSON, 1989), collagen can constitute up to 30% of the columellar tissue (as estimated by area calculations from photographs of sections).

Fine Structure of the Columellar Muscle

Two types (designated Type I and Type II) of muscle cell have been found in the columellar tissue.

Type I cells: Type I cells (Figure 2A) are the predominant muscle cell type in all species. It is probable that the cells are spindle-shaped, and cell diameters range from 3 to 6 μm in *Oxystele* spp. and *Haliotis spadicea*, 3 to 8 μm in *Turbo sarmaticus* and *Burnupena cincta*, 4 to 10 μm for *Siphonaria* spp., and 8 to 13 μm for *Bullia rhodostoma* (Table 1). Cell components of Type I cells include a random arrangement of thin and thick filaments (Figure 2B, C). In the Type I cells of all species, the dense bodies, which are sites of thin filament attachment, are relatively electron lucent (Figure 2B) with a loose granular substructure and a diameter of about 117 nm ($n = 10$ measurements per species) (Figure 2B). Electron-dense plaques, which may be attachment sites for thin filaments, are sometimes seen at the cell membrane.

Mitochondria are 1 to 2 μm long on average. In *Bullia rhodostoma* they occur along the central axis of the cell, whereas in *Turbo sarmaticus*, *Burnupena cincta*, and *Oxystele* spp. they are both central and peripheral (Figure 2A). Mitochondria are observed rarely in the muscle cells of *Haliotis spadicea* and *Siphonaria* spp. and seen only at the cell periphery. Subsarcolemmal cisternae are not well developed but are present in all species.

Thick filament diameters measured in transverse section vary within and between genera from 26 ± 7 nm in *Turbo sarmaticus* to 69 ± 20 nm in *Burnupena cincta* (Table 1). Some of this variation may be attributable to the filaments being tapered. Measurements of diameters of thick filaments in muscle cells of *Turbo sarmaticus* revealed that

some Type I cells have filaments with a mean diameter of 26 nm, whereas in others the thick filament diameters are much greater (56 nm) (Table 1). Reliable measurements of thick filament lengths from transmission electron micrographs were difficult to obtain but lengths greater than 20 μm were observed. Axial striations were seen in longitudinal sections of thick filaments of all genera examined (Figure 2D). The striations had a periodicity of about 14–15 nm (Table 1).

The diameter of the thin filaments in all species was about 6–7 nm (Table 1) as is typical for actin-containing filaments. Length measurements were impracticable because the filaments meandered in and out of the plane of the sections.

Type II cells: Type II cells, similar to those described from the columellar muscle of patellid limpets (FRESCURA & HODGSON, 1990), were observed in *Burnupena cincta* and *Bullia rhodostoma* only. These cells contain no thick filaments or dense bodies, but mitochondria, subsarcolemmal cisternae, and glycogen granules are present (Figure 3A, B). The cells have thin filaments that are bundled together by periodic electron-dense regions that give the structures a striated appearance (Figure 3A, B, C). Center-to-center spacings between the electron-dense regions are 92 and 104 nm in *Burnupena cincta* and *Bullia rhodostoma* respectively, values that are similar to those reported for patellid limpets (FRESCURA & HODGSON, 1990; Table 2).

Intercellular Regions

Intercellular regions can separate muscle cells by as much as 9 μm . These areas are often packed with collagen (Figure 2A), which is mainly organized in bundles or cross-linked arrays orientated parallel to the long axis of the muscle cells. The collagen fibrils (Figure 2E) have an axial repeat of 62 nm ($n = 50$). The diameters of the fibrils vary, having an upper limit of 70 nm. In *Burnupena cincta*, *Oxystele* spp., *Turbo sarmaticus*, and *Bullia rhodostoma*, spaces (presumed to be blood spaces) are also present between the muscle cells (Figure 3A). These spaces were not observed in *Siphonaria* spp. or *Haliotis spadicea*.

Isolated Filaments

All tissue homogenates contained thick and thin muscle filaments as well as collagen fibrils. The diameters of the thick filaments varied among the species (Table 1), ranging

Figure 2

Electron micrographs of Type I muscle cells. A. Muscle from *Burnupena cincta* showing cells with central and peripheral mitochondria (m). Scale bar = 4 μm . B and C. Higher magnifications of muscle cells from *Turbo sarmaticus* showing the arrangement of thick (T) and thin (t) filaments. Scale bars = 0.5 μm . D. Longitudinal section of thick filaments showing axial striations (arrowed). Scale bar = 0.5 μm . E. Longitudinal section through intercellular collagen fibrils. Scale bar = 0.5 μm . Key: a, attachment plate; c, collagen; d, dense body; dv, dorsoventral muscle; m, mitochondrion; s, sarcoplasmic reticulum; T, thick filaments; t, thin filaments.

Table 1

Comparison of the morphological features of the columellar muscle from a range of gastropods. Data for *Patella* sp. from FRESCURA (1991), for *Lymnaea* from PLESCH (1977). Dm = mean diameter of muscle cells; DT1 = mean diameter of thick filaments measured from sections of tissue; DT2 = mean diameter of thick filaments measured from isolated filaments; P = axial periodicities of thick filaments measured from isolated filaments (n = number of filaments with 20 periodicities measured per filament); dt = mean diameter of thin filaments.

Species	Dm (μ m)	Range (μ m)	DT1 (nm)	Range (nm)	DT2 (nm)	P (nm)	dt (nm)
<i>Patella granularis</i>	9 (n = 44)	4–13	67 \pm 27 (n = 44)	11–130	83 \pm 20	14.2 \pm 0.2	6–7 (n = 44)
<i>P. oculus</i>	9 (n = 65)	4–13	69 \pm 20 (n = 65)	26–94	84 \pm 29 (n = 16)	14.2 \pm 0.2 (n = 5)	6–7 (n = 65)
<i>P. miniata</i>	9 (n = 20)	4–13	60 \pm 20 (n = 188)	10–120	80 \pm 21 (n = 10)	14.2 \pm 0.3 (n = 5)	6–7 (n = 25)
<i>P. cochlear</i>	9 (n = 20)	4–13	64 \pm 20 (n = 58)	11–100	87 \pm 26 (n = 10)	14.3 \pm 0.4 (n = 5)	6–7 (n = 25)
<i>P. tabularis</i>	9 (n = 20)	4–13	90 \pm 35 (n = 10)	30–180	100 \pm 30 (n = 10)	14.3 \pm 0.3 (n = 5)	6–7 (n = 20)
<i>Siphonaria</i> sp.	9 (n = 20)	4–10	59 \pm 18 (n = 65)	22–137	83 \pm 15 (n = 10)	14.3 \pm 0.8 (n = 4)	6–7 (n = 20)
<i>Haliotis spadicea</i>	4 (n = 20)	3–6	60 \pm 18 (n = 21)	33–75	63 \pm 8 (n = 10)	15.2 \pm 0.6 (n = 5)	6–7 (n = 20)
<i>Oxystele</i> sp.	5 (n = 20)	3–6	56 \pm 15 (n = 20)	33–80	61 \pm 9 (n = 8)	14.7 \pm 0.3 (n = 3)	6–7 (n = 20)
<i>Turbo sarmaticus</i>	6 (n = 20)	3–8	26 \pm 7 56 \pm 15 (n = 24)	17–30 33–82	34 \pm 5 79 \pm 6 (n = 12)	14.6 \pm 0.3	6–7 (n = 20)
<i>Burnupena cincta</i>	6 (n = 20)	3–8	69 \pm 20 (n = 21)	50–90	69 \pm 27 (n = 12)	14.9 \pm 0.5 (n = 6)	6–7 (n = 20)
<i>Bullia rhodostoma</i>	9 (n = 20)	8–13	60 \pm 8 (n = 20)	30–50	78 \pm 15 (n = 8)	14.5 \pm 0.3 (n = 3)	6–7 (n = 20)
<i>Lymnaea stagnalis</i>	—	3–12	30.4 \pm 2.5	—	—	14	7

from 34 nm in *Turbo sarmaticus* to 100 nm in *Patella tabularis*. The values obtained from measurements of the isolated filaments were always slightly greater than those measured from transmission electron microscopy of intact tissue. The thick filament lengths for all species ranged between 15 and 30 μ m, but some of this variability is probably due to filaments breaking during the isolation procedure. Although typical thin filaments were seen, no striated filaments were isolated. The supernatant contained only amorphous material.

Thick filaments showed either the Bear-Selby net (BEAR & SELBY, 1956) or axial striations (Figure 3D–I) with a periodicity ranging from 14.2 to 15.2 nm (Table 1). Isolated collagen fibrils have a striated periodicity of 62 nm.

DISCUSSION

The columellar muscles of the gastropods examined in this study are predominantly composed of one type of muscle cell (designated Type 1), which has many similar fine structural features in common with Type I cells from the columellar muscle of patellid limpets (FRESCURA &

HODGSON, 1990), the shell muscle of *Lymnaea stagnalis* (PLESCH, 1977), and the anterior byssus retractor muscle (ABRM) of *Mytilus edulis* (SOBIESZEK, 1973; NICAISE & AMSELLEM, 1983). The similarities include a random arrangement of thick and thin filaments, thin filament diameters of about 6–7 nm, a paucity of dense bodies and mitochondria, and a poorly developed sarcoplasmic reticulum.

There are, however, several important differences between the Type I muscle cells of gastropods with spiral shells and the equivalent cells of patellid and siphonariid limpets. With the exception of the sandy beach whelk *Bullia rhodostoma*, muscle cell diameters are 10 to 12% smaller in the columellar muscle of gastropods with spiral shells (Table 1). In addition, the diameters of the thick filaments of the muscle cells, irrespective of whether they were measured from sections of tissue or isolated filaments, are smaller for most species of spiral-shelled gastropod (Table 1). The exception to this is *B. rhodostoma*. In all cases, thick filament diameters were greater when measured from the isolated filaments. This discrepancy is probably due in part to the different preparative procedures,

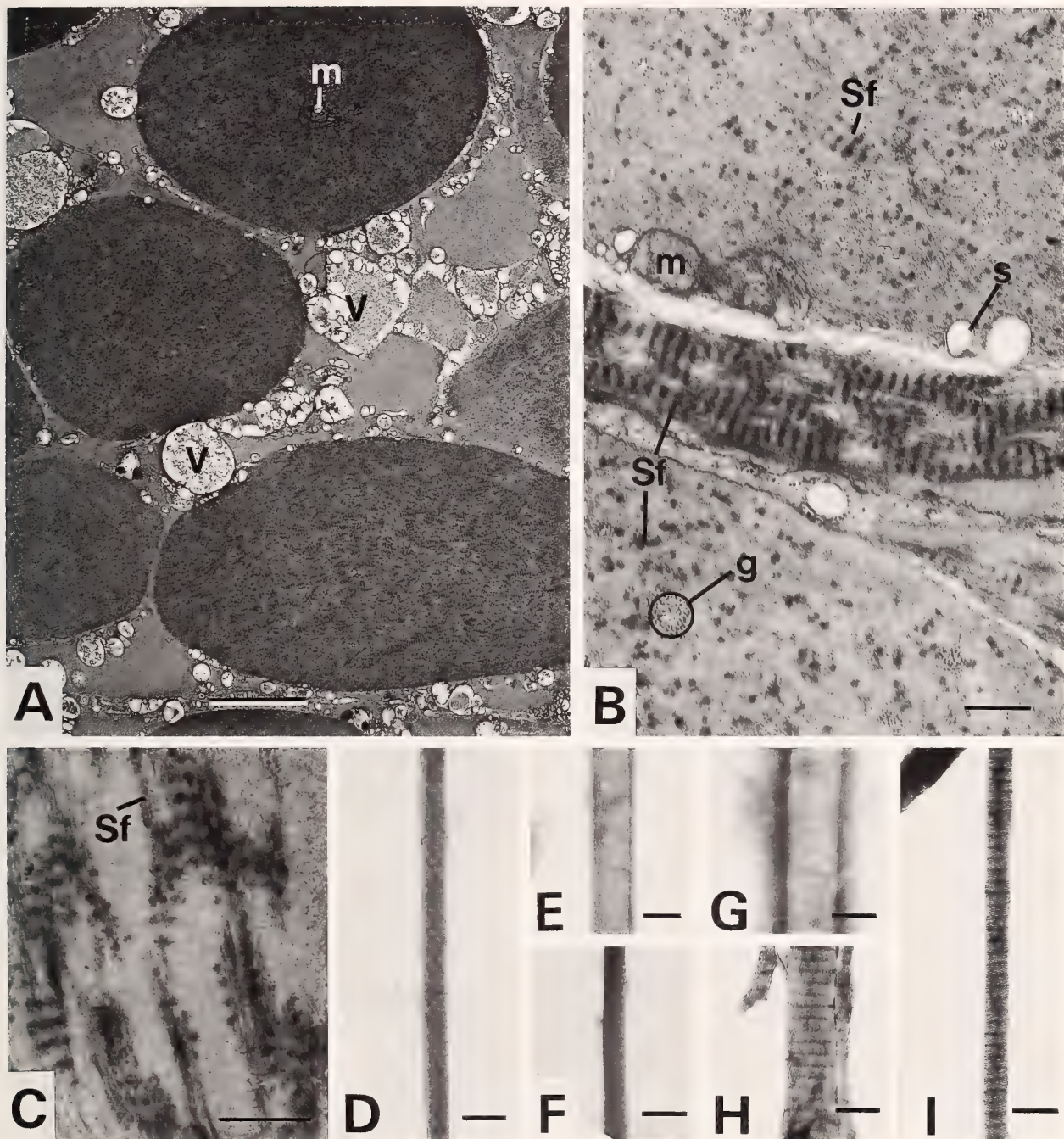


Figure 3

A-C. Sections of Type II muscle cells from the columellar muscle of *Bullia rhodostoma*. A. Transverse and oblique sections through muscle cells showing the centrally located mitochondria (m) and intercellular vesicular spaces (V) between the cells. Scale bar = 4 μ m. B and C. Higher magnification of Type II cells showing bundles of striated thin filaments (Sf), sarcoplasmic reticulum (s), and pockets of glycogen (g). Scale bars = 0.5 μ m. Figure D-I. Examples of isolated filaments: D, *Haliotis spadicea*; E, *Siphonaria capensis*; F, *Turbo sarmaticus*; G, *Patella oculus*; H, *Patella tabularis*; I, *Oxysteles sinensis*. The Bear-Selby net is apparent in D and F and axial striations in E, G, H, and I. Scale bars = 100 nm.

Table 2

Center-to-center striation spacings of bundled thin filaments from Type II muscle cells from the columellar muscle of two gastropods with spiral shells (present study) and four limpets (data from FRESCURA & HODGSON, 1990). n = number of independent bundles measured, with 3–8 striations per bundle.

Species	Spacing (mean \pm SD)	n
<i>Patella oculus</i>	135 \pm 13.0	10
<i>P. vulgata</i>	109 \pm 7.6	16
<i>P. longicosta</i>	106 \pm 8.2	10
<i>P. tabularis</i>	89 \pm 9.0	3
<i>Burnupena cincta</i>	92 \pm 15.0	10
<i>Bullia rhodostoma</i>	104 \pm 16.0	6

the procedure for isolating filaments causing less shrinkage (BENNETT & ELLIOTT, 1981; CHANTLER, 1983). CHANTLER (1983) discusses the positive relationship between the diameter of the thick filaments (and hence thick to thin filament ratios) and the force developed by muscle. Thus the combination of thicker muscle bundles and the greater diameter of thick filaments would mean that the columellar muscle of both prosobranch and pulmonate limpets should be more powerful than the equivalent muscle of gastropods with a spiral shell. Clearly this would be advantageous to limpets that inhabit areas where wave activity is most intense. The sandy beach whelk *B. rhodostoma*, which has a spiral shell, also has relatively large muscle bundles and thick filaments. This gastropod also inhabits areas of intense wave activity, where it often extends its large foot, holds it rigid, and uses it to surf up and down the beach (BROWN, 1982). A powerful columellar muscle would be of great advantage for such activity. In *Turbo sarmaticus* two populations of thick filaments with different diameters were found (Table 1). This finding is not unique, as MORRISON & ODENSE (1974) also obtained a bimodal distribution for thick filament diameters from the opaque adductors of *Arctica islandica* and *Astarte undata*. Although the functional significance of possessing two sizes of thick filament is unknown, the performance characteristics of each muscle cell type may differ.

The thick filaments from the columellar muscle of all species have an internal structure that appears to be typical of paramyosin-containing filaments. Furthermore, the axial periodicity of the filaments is about 14 nm, a value that is similar to that of paramyosin-containing filaments from other mollusks (SOBIESZEK, 1973; ELLIOTT & BENNETT, 1982; FRESCURA & HODGSON, 1990). Although the precise function of paramyosin is not known, the molecule is prevalent in muscle that has a catch mechanism (WATABE & HARTSHORNE, 1990). It is not known whether the columellar muscle of gastropods has catch properties, but such a mechanism would be energetically advantageous for both

shell support in spiral-shelled gastropods and clamping in limpets.

A further difference in the structure of the columellar muscle of gastropods with coiled shells when compared to limpets (and *Haliotis spadicea*) is the central and peripheral distribution of the mitochondria in the former and the peripheral distribution only in the latter. Centrally located mitochondria have also been reported in the pedal muscle of *Bullia rhodostoma* (DA SILVA & HODGSON, 1987) and *Nassarius kraussianus* (TRUEMAN & HODGSON, 1990). Such a distribution may improve the efficiency of ATP availability and may therefore reflect how active the muscle is. In *B. rhodostoma* and *N. kraussianus*, the pedal muscle is very active and the centrally located mitochondria are very abundant (DA SILVA & HODGSON, 1987; TRUEMAN & HODGSON, 1990). In the less active columellar muscle described in this study, mitochondria are not as abundant. FRESCURA & HODGSON (1990) described a second type of muscle cell (designated Type II) in the columellar muscle of patellid limpets. Such muscle cells contained no thick filaments but had bundles of thin filaments with a striated appearance. Type II cells were found in two species of gastropod with coiled shells, namely *Burnupena cincta* and *Bullia rhodostoma*. Table 2 shows that the periodicity of the striations in the Type II cells of these two species is similar to that reported by FRESCURA & HODGSON (1990). The function of Type II cells is still unknown and it is perplexing that they are not found in all species. Preliminary work using immunocytochemistry suggests that the filaments are composed of actin (FRESCURA, 1991) and, hence, they could also contribute to the contractile properties of the columellar muscle.

FRESCURA & HODGSON (1989, 1990) reported that collagen is abundant in the columellar tissue of patellid limpets where it may function as catch connective tissue. Intercellular collagen is also abundant in all the species examined in this study, particularly in the pulmonate limpet *Siphonaria* and the "limpet-like" archaeogastropod *Haliotis spadicea*, where it occupies all the intercellular space. In spiral-shelled gastropods, however, in addition to the intercellular collagen, vesicular spaces are present between the muscle cells. These spaces are probably blood spaces, as demonstrated by VOLTZOW (1985) in the pedal musculature of *Busycon contrarium*. Although the spaces are relatively small, they may well contribute to the mechanical properties of the columellar muscle. It is therefore possible that the columellar muscle of some gastropods with a spiral shell does not function as a true muscular hydrostat as has been suggested by TRUEMAN & BROWN (1976) and BROWN & TRUEMAN (1982).

ACKNOWLEDGMENTS

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Egg Mass and Intracapsular Development of *Cypraea caputdraconis* Melvill, 1888, from Easter Island (Gastropoda: Cypraeidae)

by

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Abstract. Egg masses and intracapsular embryos of *Cypraea caputdraconis* Melvill, 1888, are studied, documenting a discussion about the type of larval development exhibited by this species. The number of capsules per egg mass ranged between 93 and 423 ($\bar{x} = 251$) and depended on the size of the female. Each capsule contained between 502 and 1302 embryos with a mean of 880; with 251 capsules per egg mass, the average production was about 220,000 larvae per egg mass. The eggs thus produced were quite numerous and small ($\bar{x} = 102 \mu\text{m}$). Nurse cells were not observed and development culminated with the hatching of small veliger larvae.

Larval development is of the indirect type characteristic of the tropical cypraeids whose development has been previously reported. In spite of possessing the mechanism of larval dispersion here described, *Cypraea caputdraconis* has a limited geographic distribution and is restricted to the shores of Easter Island and the neighboring Sala y Gomez Island.

INTRODUCTION

The Pacific Ocean forms a barrier that can be surmounted only by effective mechanisms of dispersion over great distance (KOHN, 1967; STEHLI *et al.*, 1967; VERMEIJ, 1974, 1987; YAMAGUCHI, 1977; SPRINGER, 1982; SCHELTEMA, 1986). Two alternative mechanisms have been cited:

(a) planktonic larvae able to disperse by the currents, as is the case of many oceanic benthic species which maintain contact even with continental populations (QUAYLE, 1964; OKUBO, 1971; GERDES, 1977; SCHELTEMA, 1968, 1971, 1986); and

(b) passive transport on drifting objects or bodies (DELL, 1972; ARNAUD *et al.*, 1976; HIGHSMITH, 1985; Ó FOIGHIL, 1989) a case in which planktonic larvae are not necessary for dispersal.

The mollusk fauna of Easter Island, derived primarily from the Indo-West Pacific (EKMAN, 1953; LADD, 1960; REHDER, 1980), is endemic, due to extreme isolation in the Pacific Ocean (OSORIO & CANTUARIAS, 1989). This raises the question of what dispersal mechanisms are likely to have evolved in these mollusks, and to what extent such mechanisms may be related to their patterns of geographic distribution. An important member of this fauna is the

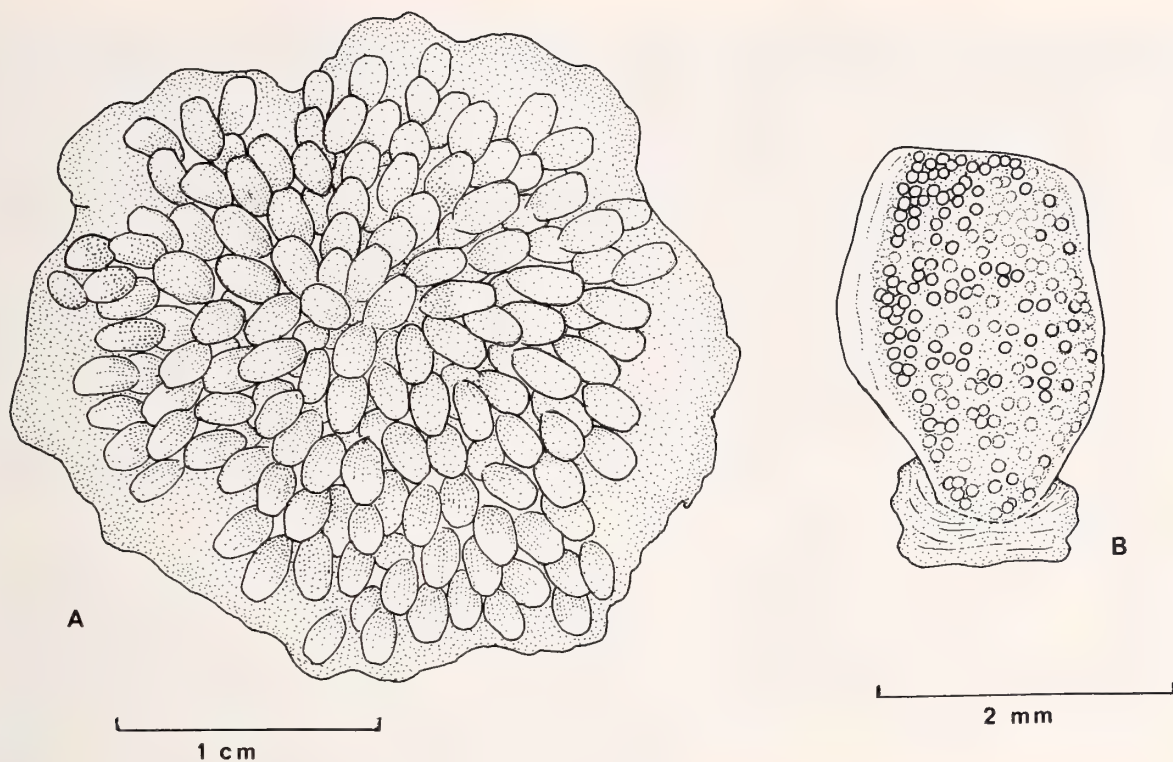


Figure 1

Egg mass of *Cypraea caputdraconis*. A. Morphology and typical pattern of grouping of egg capsules. B. Morphology of an egg capsule.

endemic Eastern Island gastropod *Cypraea caputdraconis* Melvill, 1888, which has been long used by the islanders in handcrafts or for exchange (McCOY, 1976).

To determine the pattern of larval development, and hence the dispersion mechanisms used by this gastropod, we analyze here its egg masses and some embryonic stages of intracapsular development, reporting also some field observations on the reproductive habits of these snails.

Cypraeid egg masses have been little documented. OSTERGAARD (1950) described egg masses and larval development of five *Cypraea* species from Hawaii, and BANDEL (1973) described egg masses of two Caribbean cypraeids. WILSON (1985) has reported egg masses and incubation periods, and has described hatching stages of seven cypraeids from southwest Australia with a direct embryonic development. Finally, KATOH (1989) described the life history of *C. annulus* in Okinawa, including data on fecundity, spawning frequency, and the seasonal occurrence of egg masses.

MATERIALS AND METHODS

The described material comes from Easter Island (27°09'S, 109°26'W). Field observations and collections of egg masses of *Cypraea caputdraconis* were conducted in January of 1989 and 1990. Only two complete egg masses were col-

lected in 1989; most others were destroyed, due to great difficulty in removing them from the substratum. Nonetheless, the remainder served to illuminate the general structure of the egg capsules, the number of embryos per capsule, and the intracapsular developmental stages. In the second collection, at Tepito Tecura, nine complete egg masses were obtained, allowing estimates of size and embryonic productivity in relation to the size of the incubating females.

Snails and egg masses were fixed in 10% formalin-seawater. Animals were sexed and then measured with a Vernier caliper to the nearest 0.1 mm. Egg capsules and embryos were examined and counted under a stereoscopic microscope provided with an ocular micrometer. Photographs were taken with a Wild Photoautomat, model MP5 45. A camera lucida and, occasionally, a drawing tube connected to the optical system of the microscope was used for drawings.

RESULTS

Egg Masses

The egg masses of *Cypraea caputdraconis* are found on low intertidal substrata exposed to strong wave action. They adhere firmly to the rocky substratum in cavities or

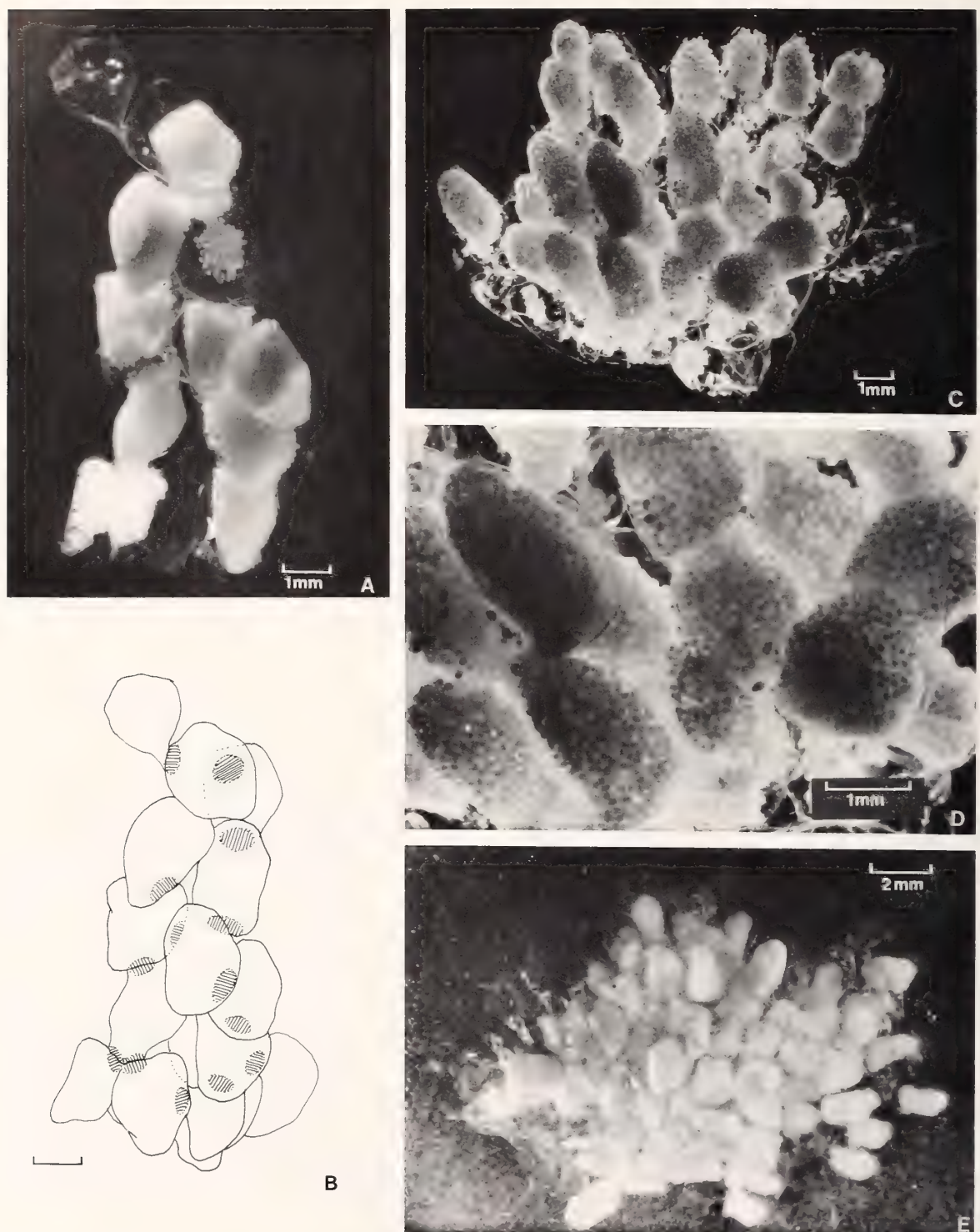


Figure 2

Egg mass of *Cypraea caputdraconis*. A and B. Group of egg capsules showing the fixation points. C. Early egg mass (stage 1). D and E. Intermediate phase of egg mass (stages 2 and 3).

crevices which offer effective protection, and from which they are difficult to remove. Other organisms found with the egg masses included polychaetes and small sea urchins (*Echinometra insularis*) and diverse algae and diatoms.

The egg masses of *Cypraea caputdraconis* (Figures 1, 2) consist of many capsules or oothecae, distributed in two to four strata, with a maximum diameter of the egg mass being 25 mm. The same egg mass may contain capsules at different developmental stages, with capsular areas of different colors, varying from white to brown as the development of the embryos progresses. Egg masses are brooded by the female, which covers them totally with her foot. Capsules are 1.8–2.8 mm long, generally oblong, and sub-rectangular in shape (Figure 1B); their walls are thin, transparent, and colorless. They adhere by means of a short, wide lamellar peduncle. Capsules of the overlying strata adhere to each other at fixation points (Figure 2B).

In nine nests found in cavities on 9 January 1990, the female was always attending the egg mass. In three cases, a male was also present; in all three, the egg masses were at the initial cleavage stage. The size of females ranged from 24 to 35.7 mm in length, and that of males from 26 to 31.7 mm.

The number of capsules per egg mass (Table 1) ranged from 93 to 423 with a mean of 251.5 (SD = 97.2) and was positively correlated with female size ($r = 0.82$; $P < 0.05$). Excluded from these calculations was an egg mass formed by only 82 capsules, since it was still at its initial stage of formation when oviposition was interrupted. For 57 oothecae, the number of embryos per capsule ranged from 502 to 1302 (mean = 879.7; SD = 158.2), but it was not correlated with the ootheca length ($r = 0.116$). An average egg mass produced by a female contains approximately 220,000 embryos.

We have been able to verify the existence of egg masses only during the summer months (December–March); observations have not yet been conducted in the remaining months of the year.

Intracapsular Development

In some egg capsules we observed uncleaved eggs with a mean diameter of 112 μm (SD = 5.1; $n = 125$). We also distinguished at least five different stages of intracapsular development (Figure 3).

In stage 1, the earliest embryonic stage observed (Figure 3A), embryos were spheric or slightly oval and 102–111 μm in diameter ($\bar{x} = 106 \mu\text{m}$), very similar in size to eggs before initiating development.

Stage 2 corresponds to clearly more advanced embryos at the phase termed pre-veliger (Figure 3B); an outline of the shell, though not coiled, covers the lower hemisphere of the embryo like a hood. In the neck region are differentiated the so-called “nuchal cells” or cephalic kidneys, transient larval structures observed in the embryonic development of other prosobranchs (PORTMANN, 1925; GALLARDO, 1973, 1977, 1979). Such organs have been pos-

Table 1

Number of egg capsules per spawn in female *Cypraea caputdraconis* of different sizes captured at Tepito Tecura (Easter Island) on 9 January 1990.

Size of female	No. of egg capsules per spawn
24.0	93
24.9	228
26.2	203
27.2	238
28.3	303
30.6	315
31.5	209
35.7	423

tulated to play an excretory function (WIERZEJSKI, 1905; Bloch, cited by KUME & DAN, 1968). The length of stage 2 embryos ranged from 144 to 161 μm , with a mean of 158 μm .

Stage 3 (Figure 3C) is an intermediate phase of intracapsular veligers, characterized by a globose shell (111–128 μm ; $\bar{x} = 119 \mu\text{m}$), which is slightly coiled, and has a pale yellow tinge. A slight outline of the operculum is evident on the foot.

The stage 4 veliger (Figure 3D) is characterized by a more pronounced coiling of the shell, which has a slightly brown tinge and ranges in size from 137 to 140 μm in length ($\bar{x} = 142.6 \mu\text{m}$). The operculum and foot are more developed, and two eye spots are present.

In stage 5 (Figure 3E, F) the shell measures 164–178 μm in length ($\bar{x} = 170.4 \mu\text{m}$). These shells are further coiled and golden brown in color. A dorsocentral beak has formed on the shell over the cephalic region, similar to that observed by DISALVO (1988) in planktonic veligers of *Concholepas concholepas*. All of the pre-hatching veligers of *Cypraea caputdraconis* contained in the same capsule were quite uniform in their morphology (Figure 3E). In 18 term oothecae, containing stage 5 larvae and having a mean length of 2.5 mm, the number of larvae per capsule varied from 502 to 1009 ($\bar{x} = 788.5 \pm 129$).

DISCUSSION

The pattern of behavior and reproduction of *Cypraea caputdraconis* resembles that of other cypraeid gastropods (OSTERGAARD, 1950; BANDEL, 1973; WILSON, 1985; KATOH, 1989). The egg mass is a group of tenuous, translucent capsules distributed in strata and incubated by the female, which protects them under her foot. Though somewhat variable in their morphology, the capsules resembled those described by BANDEL (1973) for *C. cinerea*.

The data obtained in the present study suggest a pattern of indirect development with phytoplanktotrophic pelagic larvae. This conclusion is supported by the large number of embryos per egg mass, the relatively small size of the

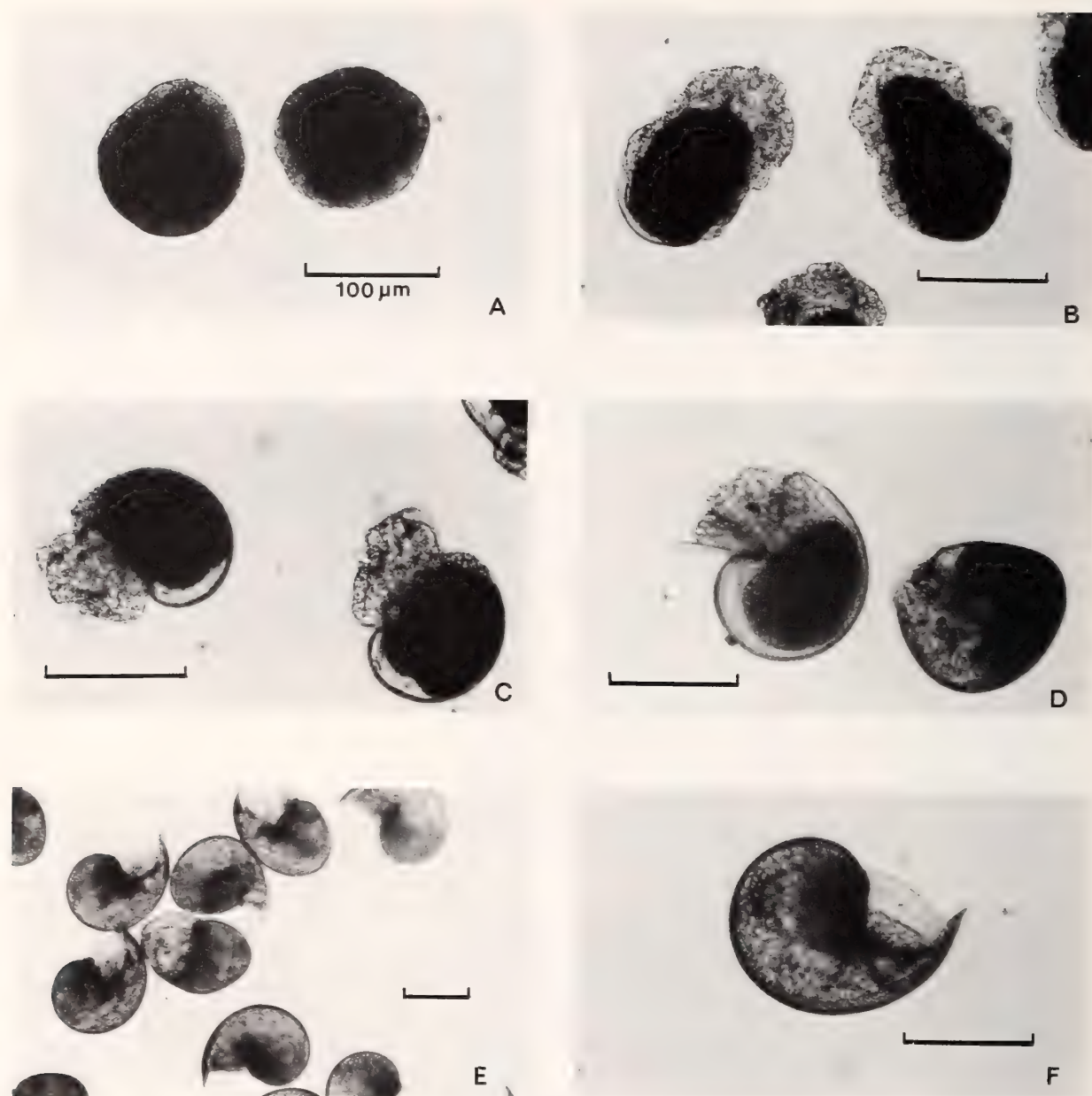


Figure 3

Stages of intracapsular development. *Cypraea caputdraconis*. A. Early embryos (stage 1). B. Pre-veliger phase (stage 2). C. Intermediate veliger phase (stage 3). D. Veliger larvae (stage 4). E and F. Terminal veliger larvae, prior to eclosion (stage 5). Scale = 100 μ m.

egg, the absence of nurse cells, and the small size of the larva at its terminal stage of intracapsular development, prior to hatching. These features roughly coincide with observations on other tropical cypraeid egg masses releasing planktonic larvae (OSTERGAARD, 1950; D'ASARO, 1970; KAY, 1960; BANDEL, 1973). Indirect larval development is the dominant pattern among *Cypraea*, and particularly characterizes cypraeids inhabiting tropical waters (WILSON,

1985). Species with a planktonic larval stage hatch 10,000 to 500,000 veliger larvae per egg mass, usually with the production of hundreds in each capsule.

These species clearly contrast with directly developing species inhabiting temperate seas on the south coast of Australia and in South Africa (WILSON, 1985). The species from southern Australia described by Wilson are characterized by the development of a single embryo per oo-

theca, which consumes all other remaining eggs that serve as nurse cells. In each spawn, females produce 50 to 100 offspring in the genus *Notocypraea* and 150 to 300 in *Zoila* and *Austrocypraea*. The same occurs with *Cypraeovula* in South Africa. According to data reported for tropical cypraeids with planktonic larvae (WILSON, 1985), we might have expected that the brooding time of *Cypraea caputdraconis* would be relatively short. In tropical cypraeids it fluctuates between 11 and 18 days, while temperate species with direct development may require from 45 to 55 days to complete intracapsular development.

The existence of planktonic larvae in *Cypraea caputdraconis* raises the question of capacity for dispersal during their planktonic drift. The open ocean of the tropical Pacific forms a barrier for dispersal, which can be overcome only by species possessing the ability for long distance transport. Among the mollusks of the Indo-Pacific there are species with a strictly continental distribution and oceanic species that can inhabit both continental and oceanic islands (TAYLOR, 1971; REID, 1985). The tendency to lack planktonic larvae is more marked among continental gastropods, whereas their oceanic counterparts tend to retain the primitive modality of planktonic larval development (PERRON & KOHN, 1985; VERMEIJ, 1987).

The existence of planktonic larvae among gastropods inhabiting oceanic islands is supported by our findings in *Cypraea caputdraconis*. In turn, direct development has been reported for cypraeids of continental coasts, such as those of Australia and South Africa (WILSON, 1985). Notwithstanding, it must be noted that the distribution of *C. caputdraconis* is limited to Easter Island and Sala y Gomez (OSORIO & CANTUARIAS, 1989) and the species has not been reported from continental shores. This fact suggests that larvae of *C. caputdraconis* are not successfully dispersed over great distances, but rather that dispersal is restricted to a local scale within the oceanic insular area in which the species is found.

ACKNOWLEDGMENTS

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New Morphologic and Geographic Data on the Neritid Gastropod *Nerita* (*Theliostyla*) *triangulata* Gabb, 1869, from the Eocene of the Pacific Coast of North America

by

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Abstract. Abundant and exceptionally well-preserved specimens of the neritid gastropod *Nerita* (*Theliostyla*) *triangulata* Gabb, 1869, from brackish-marine deposits of the middle Eocene (“Domengine Stage”) Delmar Formation, northern San Diego County, show previously unreported morphologic features. A tricarinate body whorl is a major characteristic of the species, but on some of the more mature Delmar Formation specimens the three carinae become faint to obsolete as they approach the outer lip. Comparative studies reveal three subjective synonyms of *Nerita* (*Theliostyla*) *triangulata*. They are *Nerita triangulata* Gabb var. *oregonensis* Merriam & Turner, 1937, from lower Eocene (“Capay Stage”) strata, southwestern Oregon, *Nerita quadrangulata* Weaver & Kleinpell, 1963, from upper Eocene (“Tejon Stage”) strata, southern California, and *Nerita* n. sp. Clark, 1938, from upper Eocene (“Tejon Stage”) strata, northern California. The new geographic range of *N. (T.) triangulata* is San Diego to southwestern Oregon, and the new geologic range is upper lower Eocene (“Capay Stage”) to upper Eocene (“Tejon Stage”).

Nerita (*Theliostyla*) *triangulata* shows close affinities with a few southern European species. *Theliostyla* is probably a Tethyan immigrant that arrived on the Pacific coast of North America during the early Eocene.

INTRODUCTION

The Pacific coast of North America neritid gastropod *Nerita* (*Theliostyla*) *triangulata* Gabb, 1869, is a common constituent of Eocene molluscan faunas in very shallow marine or brackish-water deposits. By all accounts, it is a species characterized by three strong widely spaced carinae on the body whorl. Recent collecting, however, has yielded exceptionally well-preserved specimens that show a gradation from three strong carinae on the early part of the body whorl to faint carinae to no carinae on the late part of the body whorl. It is the purpose of this present study to report on this morphologic variation. All reported Paleogene species of *Nerita* from the Pacific coast of North America also were reviewed, and three taxa were detected as subjective synonyms of *N. (T.) triangulata*.

Nerita (*Theliostyla*) *triangulata* has no apparent ancestor among indigenous Paleocene or Cretaceous faunas but does

have relatives in the lower Eocene of southern Europe. *Nerita pentastoma* DESHAYES (1866:19, pl. 66, figs. 7–9; COSSMANN & PISSARRO, 1910–1913:pl. 5, fig. 38–5; SZÖTS, 1953:141, pl. 2, figs. 1, 2), from the lower Eocene of the Paris Basin, France, and of Hungary closely resembles *N. (T.) triangulata* and should be assigned to the subgenus *Theliostyla*. *Nerita tricarinata* LAMARCK (1804:94; 1806:pl. 14, figs. 4a, b; DESHAYES, 1837:pl. 19, figs. 9, 10; COSSMANN & PISSARRO, 1910–1913:pl. 5, fig. 38–4; COSSMANN, 1925:pl. 6, figs. 41, 42; PALMER, 1977:vélin 47, figs. 7a, b) from the lower Eocene of the Paris Basin, France, also closely resembles *N. (T.) triangulata*. GLIBERT (1962:100) assigned *N. tricarinata* to the subgenus *Theliostyla*. *Nerita heberti* SZÖTS (1953:141–142, pl. 2, figs. 3–5) and *Nerita hantkeni* SZÖTS (1953:142, pl. 2, figs. 6, 7), both from the lower Eocene of Hungary closely resemble *N. (T.) triangulata* and appear to be referable to the subgenus *Theliostyla*.

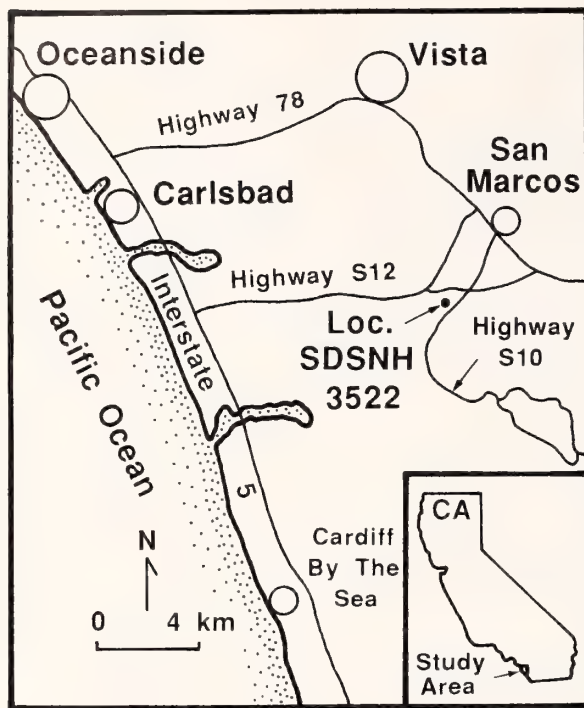


Figure 1

Index map of locality SDSNH 3522 in northern San Diego County.

Theliostyla probably originated in the Old World Tethyan paleobiotic province and immigrated to the Pacific coast of North America during the early Eocene. In addition to the appearance of *Nerita* (*Theliostyla*) *triangulata* on the Pacific coast of North America during the early Eocene, another possible species of *Nerita* (*Theliostyla*) appeared in this area during this time. WOODS & SAUL (1986) reported a single specimen of *N. (T.)* n. sp. (?) from the Sepultura Formation near Punta Rosarito, Baja California, Mexico. They questionably assigned this formation to the upper Paleocene. FLYNN *et al.* (1989) assigned these strata to the lower Eocene ("Capay Stage"). The specimen of WOODS & SAUL (1986) seems to be allied to *N. (T.) crooki* Clark, 1938, known from the upper Eocene Markley Formation on Pleasant Creek, Solano County, northern California.

The molluscan stages used in this report stem from CLARK & VOKES (1936), who proposed five mollusk-based provincial Eocene stages, namely, "Meganos," "Capay," "Domengine," "Transition," and "Tejon." The stage names are in quotes because they are informal terms. GIVENS (1974) modified the use of the "Capay Stage," and it is in this modified sense that the "Capay Stage" is used herein.

Abbreviations used for catalog and/or locality numbers are: CAS, California Academy of Sciences, San Francisco; LACMIP, Los Angeles County Museum of Natural History, Invertebrate Paleontology Section; SDSNH, San Di-

ego Society of Natural History; SUPTC, Stanford University Paleontology Type Collection (now housed at CAS); UCMP, University of California Museum of Paleontology, Berkeley.

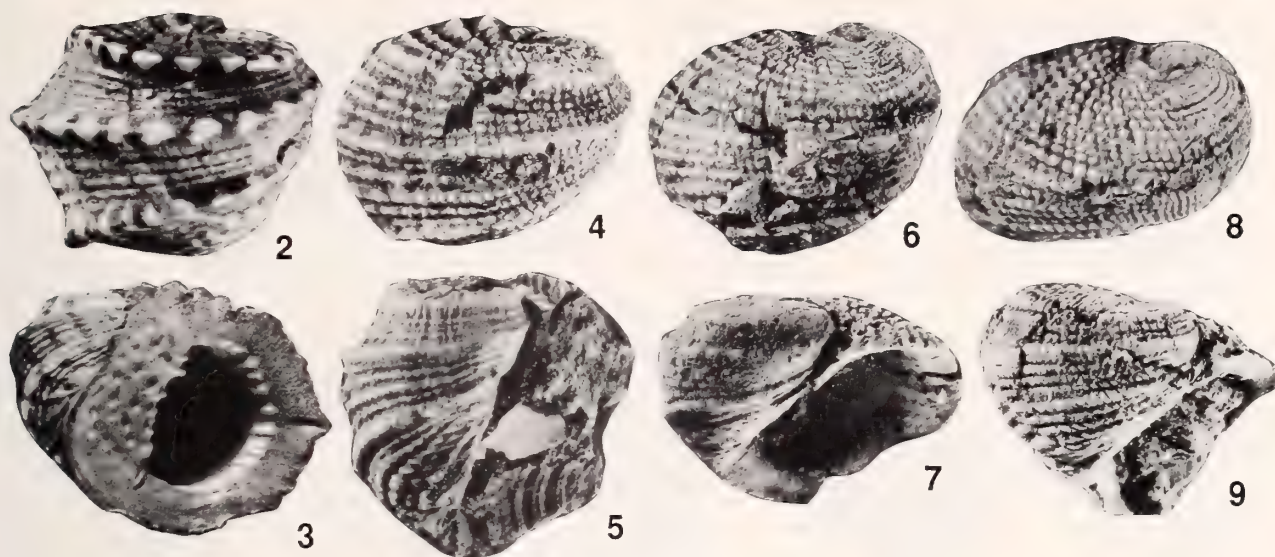
NEW GEOGRAPHIC OCCURRENCE

The new specimens of *Nerita* (*T.*) *triangulata* were found a few kilometers west of the city of San Marcos, northern San Diego County (Figure 1) at locality SDSNH 3522. This locality is 1220 feet (372 m) north and 2180 feet (665 m) east of the southwest corner of section 17, T12S, R3W, U.S. Geological Survey, San Marcos, California, 1968 (photorevised 1983), 7.5-minute topographic quadrangle, at elevation 570 feet (174 m). Approximately 7.5 m of interbedded sandstone and muddy siltstone within a channel complex were temporarily exposed in 1989 by construction work in the immediate vicinity of the locality (*i.e.*, the Laurels housing development project). Numerous mollusks and abundant leaves were found at locality SDSNH 3522 at the bottom of the exposure in greenish gray, poorly sorted, very fine- to coarse-grained sandstone with clayey matrix. Angular grains of quartz are common. Outcrops of granitic basement are within 200 m of locality SDSNH 3522.

The lithology, sedimentary structures, and fossil content at locality SDSNH 3522 agree very closely with the "green mudstone and sandstone" lithology of lithofacies 3 of EISENBERG & ABBOTT (1991), who did a detailed study of the various middle Eocene paralic environment rock types that crop out in northern San Diego County. They assigned their lithofacies 3 to the Delmar Formation, which is correlative to the upper lower to lower middle Eocene "Domengine Stage" (GIVENS & KENNEDY, 1979).

Mollusks associated with the new specimens of *Nerita* (*T.*) *triangulata* include the gastropods *Potamides carbonicola* Cooper, 1894, and *Umpquaia oregonensis*, Turner, 1938, and the bivalves *Acutostrea idriaensis fettkei* (Weaver, 1912), *Pelecypora aequilateralis* (Gabb, 1869), and *Corbula* (*Cuneocorbula*) *torreyensis* Hanna, 1927. All of these mollusks, including *N. (T.) triangulata*, are diagnostic of brackish-marine conditions (GIVENS, 1974; GIVENS & KENNEDY, 1976, 1979; SQUIRES, 1991; SQUIRES & DEMÉRÉ, 1991). The mollusks at locality SDSNH 3522 were transported a short distance and concentrated within a channel complex, along with land-plant remains. The shoreline must have been very nearby because the shells show no evidence of abrasion or sorting. The shoreline was probably irregular with basement crystalline headlands and protected lagoon, and this interpretation would be in keeping with what other workers have reported for the middle Eocene shoreline in the San Diego area (LOHMAR & WARME, 1979; EISENBERG, 1985; SQUIRES & DEMÉRÉ, 1991).

Nerita (*Theliostyla*) *triangulata* has been previously reported from San Diego County. HANNA (1927) and GIVENS & KENNEDY (1979) reported the species from the Delmar Formation near Torrey Pines State Park. GIVENS



Explanation of Figures 2 to 9

Figures 2-9. *Nerita (Theliostyla) triangulata* Gabb, 1869, locality SDSNH 3522, Delmar Formation, northern San Diego County, southern California. Figure 2: hypotype SDSNH 406777, abapertural view, $\times 6$. Figure 3: hypotype SDSNH 406787, apertural view, $\times 4.4$. Figures 4, 5: hypotype SDSNH 43472, abapertural and lateral views, $\times 3.1$. Figures 6, 7: hypotype SDSNH 43473, abapertural and oblique apertural views, $\times 2.9$. Figures 8, 9: hypotype SDSNH 43474, slightly crushed, abapertural and lateral views, $\times 2.7$.

& KENNEDY (1976) also reported the species from probable middle Eocene ("Domengine Stage") rocks near the city of Vista in northern San Diego County.

Nerita n. sp.: CLARK, 1938:701, pl. 4, fig. 6.

Nerita quadrangulata WEAVER & KLEINPELL, 1963:183, pl. 23, fig. 1.

SYSTEMATIC PALEONTOLOGY

Family NERITIDAE Rafinesque, 1815

Subfamily NERITINAE Rafinesque, 1815

Genus *Nerita* Linné, 1758

Type species: By subsequent designation (MONTFORT, 1810),
Nerita peloronta Linné, 1758.

Subgenus *Theliostyla* Mörch, 1852

Type species: By subsequent designation (KOBELT, 1879),
Nerita albicilla Linné, 1758.

Nerita (Theliostyla) triangulata Gabb, 1869

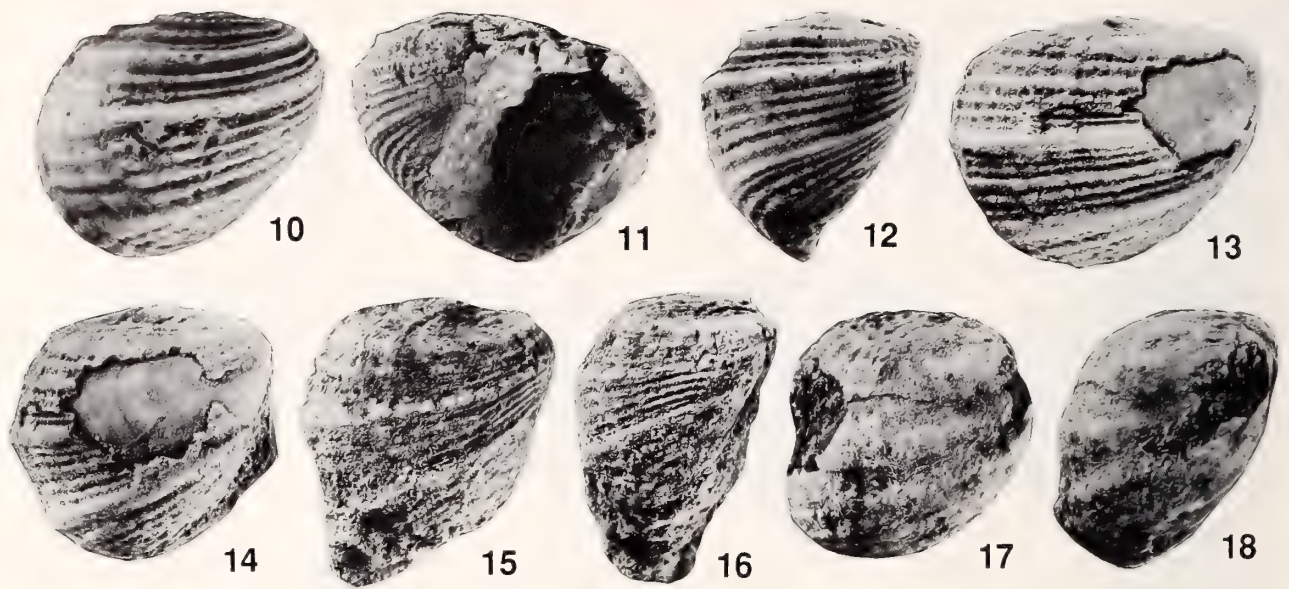
(Figures 2-18)

Nerita (Theliostyla) triangulata GABB, 1869:170, pl. 28, figs. 52, 52a; VOKES 1939:182, pl. 22, figs. 31, 33, 34; GIVENS, 1974:61, pl. 5, fig. 4; GIVENS & KENNEDY, 1976:960, 963, pl. 1, figs. 1-4; SQUIRES, 1987:23, fig. 14.

Nerita triangulata Gabb: ARNOLD, 1910:14, pl. 14, figs. 12, 12a (figs. repeated in ARNOLD & ANDERSON, 1910:pl. 26, figs. 12, 12a); HANNA, 1927:301, pl. 46, figs. 11, 12, 16, 17; MOORE, 1968:28, pl. 12a.

Nerita triangulata Gabb var. *oregonensis* MERRIAM & TURNER, 1937:104, pl. 6, fig. 5; TURNER, 1938:95, pl. 19, figs. 10-12; WEAVER, 1942 [1943]:295-296, pl. 64, figs. 10, 13.

Supplementary description: Small sized, broader than high, with rapidly expanding body whorl. Spire very low to flattened, apex usually depressed below gently sloping dorsal surface. Dorsal surface with four to six noded spiral ribs (excluding carina on shoulder) that become coarser toward outer lip. Posterior part of dorsal surface of body whorl elevated and somewhat carinate. Body whorl with three widely spaced, somewhat nodose carinae. On some specimens larger than about 9.5 mm height, carinae on body whorl become faint to obsolete toward outer lip. Degree of obsolescence of carinae increases with size of shell. Medial carina slightly stronger than other two carinae. On a few specimens, body whorl shoulder rounded, and spiral cord in middle of interspace between shoulder and medial carina can approximate or exceed strength of shoulder. Spiral ribs in interspaces of carinae become stronger and more nodose toward outer lip. Juvenile specimens faintly nodose, late juvenile specimens nodose, and a few late-mature specimens strongly beaded. Some specimens with a fine reticulate sculpture pattern in interspaces near inner lip. Interspace between shoulder and medial carinae with two spiral ribs near inner lip and three to four spiral ribs on late part of body whorl. Interspace between medial and anteriormost carinae with two to three spiral ribs near inner lip and three to five on late part of body whorl. Interspace between anteriormost carina and



Explanation of Figures 10 to 18

Figures 10–18. Type material of subjective synonyms of *Nerita* (*Theliostyla*) *triangulata* Gabb, 1869. Figures 10–12: *Nerita triangulata* Gabb var. *oregonensis* Merriam & Turner, 1937, Lookingglass Formation, Douglas County, southwestern Oregon, holotype UCMP 33204, abapertural, apertural, and lateral views, $\times 3.3$. Figures 13–16: *Nerita quadrangulata* Weaver & Kleinpell, 1963, undifferentiated Sacate-Gaviota formation, Santa Barbara County, southern California. Figures 13, 14: holotype CAS 66550.01 (ex SUPTC 9175), apertural view, $\times 2.7$. Figures 15, 16: paratype CAS 66550.02 (ex SUPTC 9175a), abapertural and lateral views, $\times 3.3$. Figures 17, 18: *Nerita* n. sp. Clark, 1938, Markley Formation, northern California, hypotype UCMP 30490, abapertural and lateral views, $\times 2.5$.

base of body whorl with two to five (rarely six) fairly prominent spiral ribs with elongate or irregular nodes.

Aperture large, quadrate. Outer lip flared, with grooves where intersected by three body-whorl carinae, and with or without shallow grooves where intersected by spiral ribs on the exterior of the body whorl. Outer lip interior with 11 to 15 narrow, elongate teeth not extending to outer lip periphery; interspaces between teeth generally align with grooves along outer lip periphery; teeth usually widely spaced but a few can be paired. Inner lip with six to seven teeth. Two posteriormost teeth stronger than rest, with tooth next to posteriormost tooth strongest. Three to four small, subequal teeth medially. Anteriormost tooth blunt and well developed only in larger specimens. Deck with 16 to 23 small tubercles, arranged very loosely in rows somewhat coincident with inner lip teeth. Two posteriormost teeth can extend onto deck area as ridges, with tooth next to posteriormost the strongest.

Original color pattern with alternating axial bands of white and brown becoming chevron shaped on crests of body whorl carinae and forming zig-zag pattern in interspaces of carinae, especially in interspace near base of body whorl. Chevrons point toward outer lip on crests of carinae. Color pattern best developed on specimens that are not strongly noded or beaded.

Discussion: Of the 61 specimens of *Nerita* (*Theliostyla*) *triangulata* from locality SDSNH 3522, seven have carinae that become faint to obsolete with growth. An example of faint carinae on the late part of the body whorl is shown in Figure 6, and an example of no carinae in that area is shown in Figure 8. Both of these specimens, however, have three strong carinae on the early part of the body whorl (Figures 7, 9, respectively). The late part of the body whorl of the specimen illustrated in Figure 8 resembles the holotype (and only known specimen) of *Nerita* (*Theliostyla*) *crooki* CLARK (1938:700, pl. 4, figs. 1, 2) from the upper Eocene Markley Formation on Pleasant Creek, Solano County, northern California. *Nerita* (*T.*) *crooki*, however, has no carinae on the early part of the body whorl. This species is assigned herein to the subgenus *Theliostyla* because of the presence of tubercles on the deck.

GIVENS & KENNEDY (1976) collected five, exceptionally well-preserved specimens of *Nerita* (*T.*) *triangulata* from a locality in very shallow marine or brackish-water deposits of probable middle Eocene age ("Domengine Stage"), near the city of Vista in northern San Diego County. Locality SDSNH 3522 is about 3.8 km to the south of their locality. Their specimens are all less than about 9.5 mm in height and have a tricarinate body whorl.

MERRIAM & TURNER (1937) reported multiple speci-

mens (exact number unknown) of *Nerita triangulata* var. *oregonensis* Merriam & Turner, 1937, from the lower Eocene ("Capay Stage") Capay Formation, northern California, and from the upper Umpqua Formation near Glide, Douglas County, southwestern Oregon. Revisions of stratigraphic nomenclature in southwestern Oregon now place the localities of the Glide section from which *N. t. oregonensis* has been collected in the lower Eocene ("Capay Stage") Lookingglass Formation (BALDWIN, 1974, 1975; THOMS, 1975; MILES, 1981).

MERRIAM & TURNER (1937) and TURNER (1938) reported that the body whorl of *Nerita triangulata* var. *oregonensis* is less sharply angulate and has weaker spiral ribs than does *N. (T.) triangulata*. It is not clear from the original description of *N. t. oregonensis* if MERRIAM & TURNER (1937) were describing a morphologic variant or a new subspecies. Their holotype (Figures 10–12), however, is very much like the Delmar Formation specimen shown in Figures 4 and 5. The Oregon specimen is less nodose than the Delmar Formation specimen because the Oregon specimen is a worn shell. In addition, the Oregon specimen is slightly smaller, and nodosity in *N. (T.) triangulata* is weaker on small specimens. I believe that *N. triangulata* var. *oregonensis* and *N. (T.) triangulata* are conspecific.

WEAVER & KLEINPELL (1963) reported *Nerita quadrangulata* Weaver & Kleinpell, 1963, from the upper Eocene ("Tejon Stage") undifferentiated Sacate-Gaviota formation, Nojoqui Creek area, Santa Barbara County, southern California. They reported that *N. quadrangulata* differs from *N. (T.) triangulata* by having a much weaker body-whorl shoulder, a fourth and nearly equal carina just anterior, and five rather than four spiral ribs between the two anteriormost carinae. The holotype of *N. quadrangulata* (Figures 13, 14) does have a somewhat weak body-whorl shoulder in the vicinity of the outer lip. It is difficult to determine how strong the body-whorl shoulder was in the early part of the whorl because a large portion of shell is missing there. The best preserved paratype of *N. quadrangulata* (Figures 15, 16), however, shows the characteristic tricarinate body whorl in both the early and later parts of the body whorl. Also, given the variability in morphology seen in the Delmar Formation specimens of *N. (T.) triangulata*, the variability in the strength of the shoulder in *N. quadrangulata* is not sufficient to distinguish this species from *N. (T.) triangulata*. In addition, *N. (T.) triangulata*, like *N. quadrangulata*, can have as many as five spiral ribs between the two anteriormost carinae; GABB (1869) also noted this feature on *N. (T.) triangulata*.

CLARK (1938) reported a single, poorly preserved specimen of *Nerita* n. sp. from the upper Eocene Markley Formation on Pleasant Creek, Solano County, northern California. This worn specimen of *Nerita* n. sp. has three faint carinae on the body whorl (Figures 17, 18) and is judged to be *N. (T.) triangulata*.

There are three other named species of the genus *Nerita*

from Eocene rocks along the Pacific coast of North America. Two, *Nerita cowlitzensis* DICKERSON (1915:58–59, pl. 5, figs. 7a, b) and *Nerita washingtoniana* WEAVER & PALMER (1922:28–29, pl. 11, fig. 4), are from the upper middle Eocene Cowlitz Formation, southwest Washington, and the third, *Nerita vokesi* DURHAM (1944:156, pl. 17, figs. 11, 12), is from the *Molopophorus stephensoni* megafaunal zone of northwest Washington. ARMENTROUT (1975) assigned this zone to his upper Eocene Galvinian Molluscan Stage. *Nerita cowlitzensis* differs from *N. (T.) triangulata* in the following features: smaller, nodose only on the dorsal surface, body whorl with only minute sculpture, and aperture more elongate. *Nerita washingtoniana* differs from *N. (T.) triangulata* in the following features: much smaller, smooth body whorl, and a possible divaricate color pattern. *Nerita vokesi* differs from *N. (T.) triangulata* in the smooth body whorl, only four subequal inner lip teeth, and a much more variable color pattern. It is important to mention that the inner lip teeth of *N. (T.) triangulata*, *N. cowlitzensis*, and *N. washingtoniana* are very similar.

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A New Aeolid (Gastropoda: Nudibranchia) from the Atlantic Coasts of the Southern Iberian Peninsula

by

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Abstract. A new species of aeolid nudibranch, *Cuthona willani*, is described from the Atlantic coasts of the southern Iberian Peninsula. The swellings of the rhinophores and oral tentacles, the shape of cerata, and the coloration separate *C. willani* from the remaining Lusitanian, Mediterranean, and Mauretanian known species of the genus.

INTRODUCTION

A new species of the aeolid genus *Cuthona* Alder & Hancock, 1855, has been described recently from the Atlantic coasts of the southern Iberian Peninsula by GARCÍA *et al.* (1991). In this paper, we describe another species of the same genus from the same geographical area.

Family TERGIPEDIDAE Thiele, 1931

Cuthona Alder & Hancock, 1855

Cuthona willani Cervera, García-Gómez &
López-González, sp. nov.

(Figures 1-3)

Material: Holotype: One specimen, 12 mm in length, collected intertidally, El Portil (Huelva, Spain) (37°12'40"N, 7°7'50"W), September 1986. This specimen, which was not dissected, has been deposited in the collections of the Museo Nacional de Ciencias Naturales (MNCN) of Madrid, catalogue number 15.05/0763.

Paratypes: One specimen, 11 mm in length, collected concurrently with the holotype, has been deposited in the Laboratorio de Biología Marina (LBM), Departamento de Fisiología y Biología Animal, Universidad de Sevilla. One specimen, 3 mm in length, collected by SCUBA at 20 m depth in Sagres, Portugal (37°N, 8°55'W), during the International Expedition "ALGARVE 88," May 1988. This specimen has been deposited in the LBM, Departamento de Fisiología y Biología Animal, Universidad de Sevilla.

A color slide of this living specimen of *Cuthona willani* is on file at the LBM, Universidad de Sevilla.

Description: The body is typically aeolidiform (Figure 1A, B) and slightly narrower than the foot, tapering posteriorly in a relatively long and pointed tail. The foot corners are square. The oral tentacles are cylindrical, with a slight swelling in their middle part, and long, nearly as long as the rhinophores (Figure 1A, B, E). The rhinophores are long, smooth, and slightly enlarged at their base. They have a similar swelling to that of the oral tentacles at the apical half (Figure 1A, B). The cerata are arranged in 10 to 13 dorsolaterally oblique rows on either side of the body (Figure 2A). The postcardial rows of cerata on each side are arranged alternately with regard to those on the opposite side. The ceratal half formula is I 1-2, II 2-3, III 3-4, IV 3-5 (precardial), V 4-5, VI 4-5, VII 4-6, VIII 3-7, IX 2-6, X 1-4, XI 2-4, XII 3, XIII 3 (postcardial). The cerata have a conspicuous subapical globular enlargement, which is more developed in the largest (medial) cerata than in the smallest (lateral) ones. The cerata have another less conspicuous swelling before narrowing at the base (Figure 1C). The tips of the cerata may appear rounded (when an animal is undisturbed, the apex of the cnidosac is retracted) (Figure 1D, a) or pointed (when an animal is disturbed, the apex of the cnidosac is extended) (Figure 1D, b). The anus is acleiopect and the genital pore is under the second row of cerata on the right side (Figure 2A).

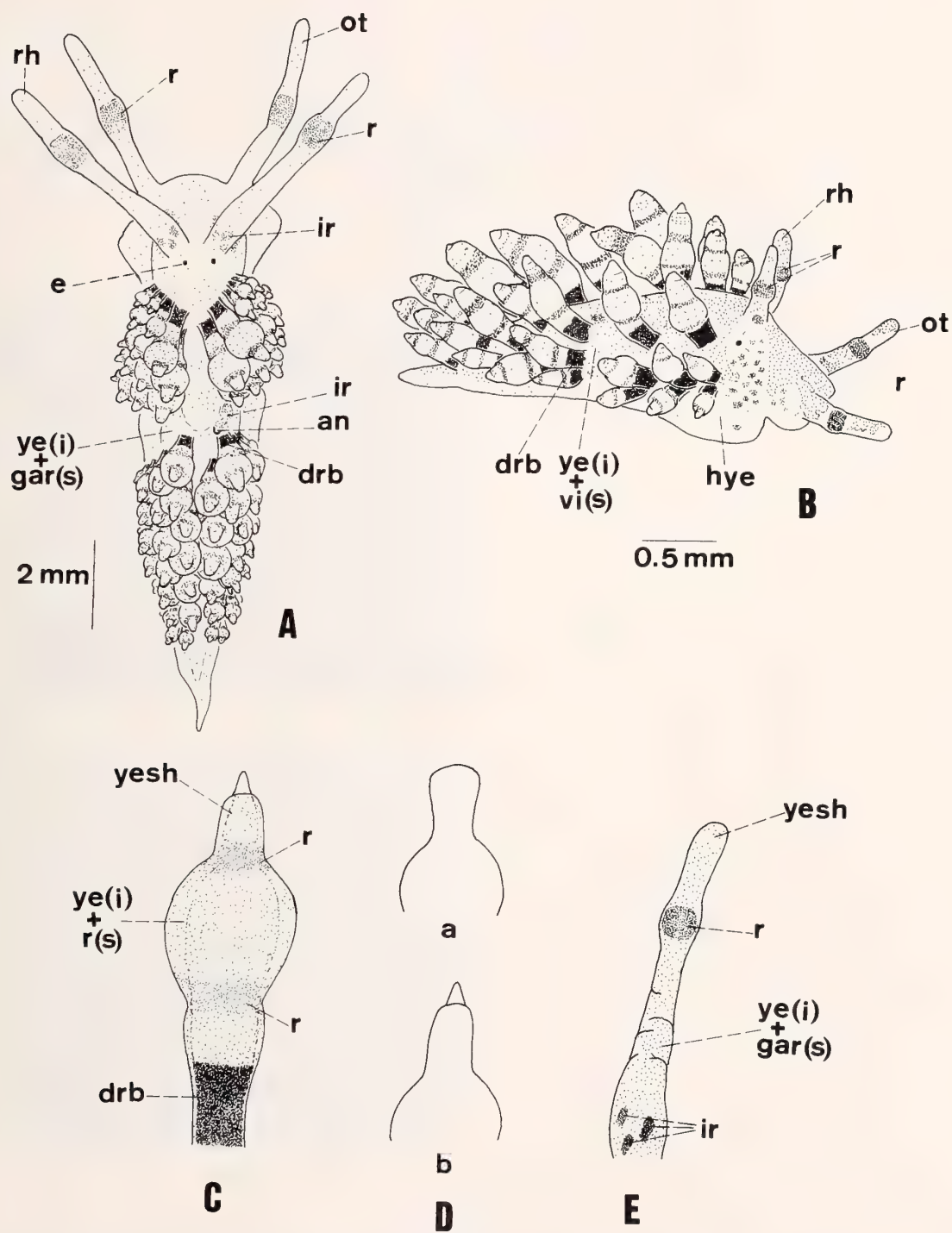


Figure 1

Cuthona willani sp. nov. A. Dorsal view of 11-mm adult specimen. B. Lateral view of 3-mm juvenile specimen. C. Detail of a cerata. D. Variability of the apical shape of the cerata—(a) apex of cnidosac extended, (b) apex retracted. E. Detail of a rhinophore. Key: an, anus; drb, dark reddish brown; e, eye; gar(s), garnet (superficial); hye, hyaline yellow; ir, iridescent red; ot, oral tentacle; r, red; vi, violet; ye(i), yellow (internal); yesh, yellowish.

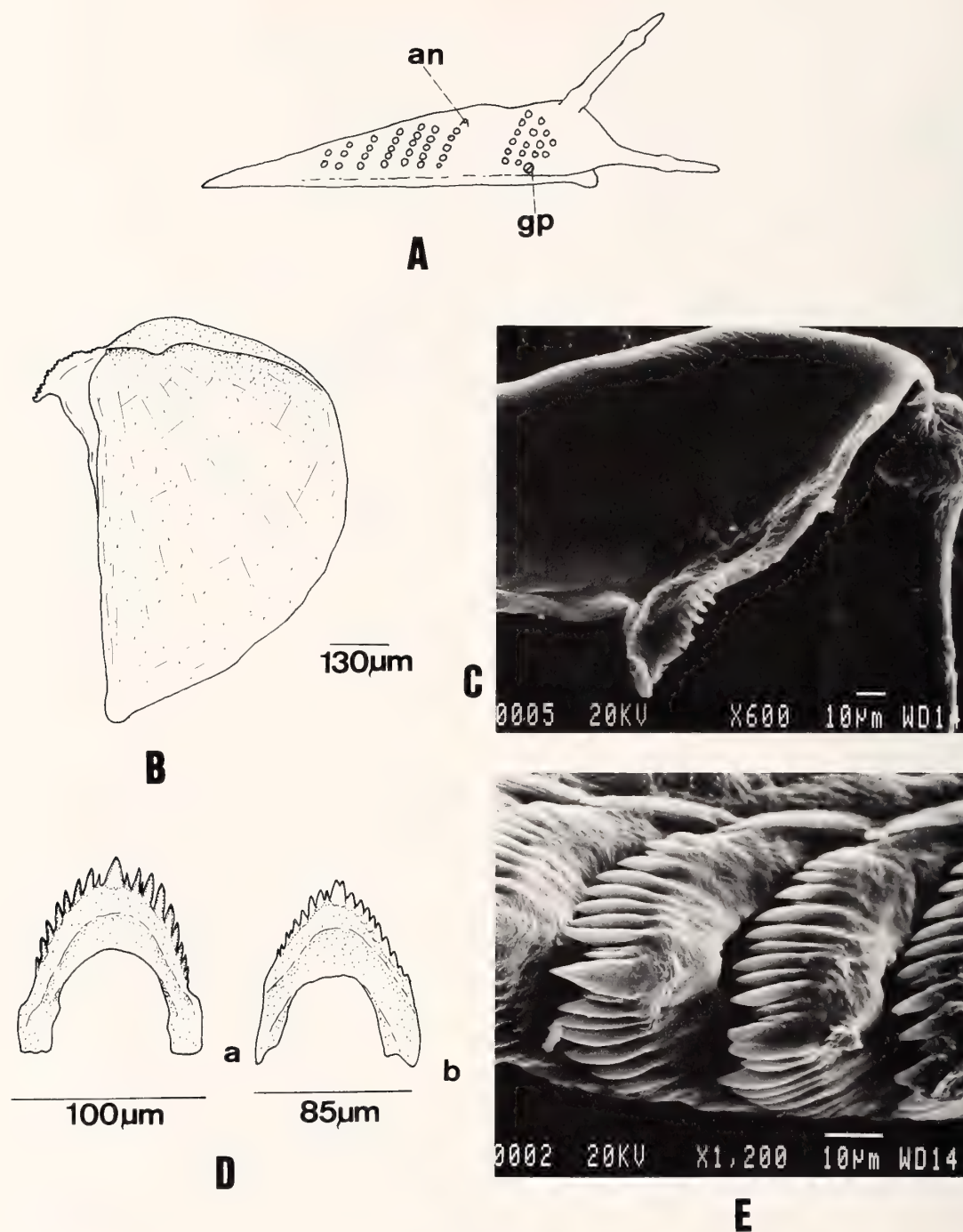


Figure 2

Cuthona willani sp. nov. A. Schematic arrangement of cerata. B. Jaw. C. Detail of the masticatory border of jaw. D. Second (a) and eighth (b) radular teeth of the 11-mm specimen. E. Scanning electron micrograph of some radular teeth of the same specimen. Key: an, anus; gp, genital pore.

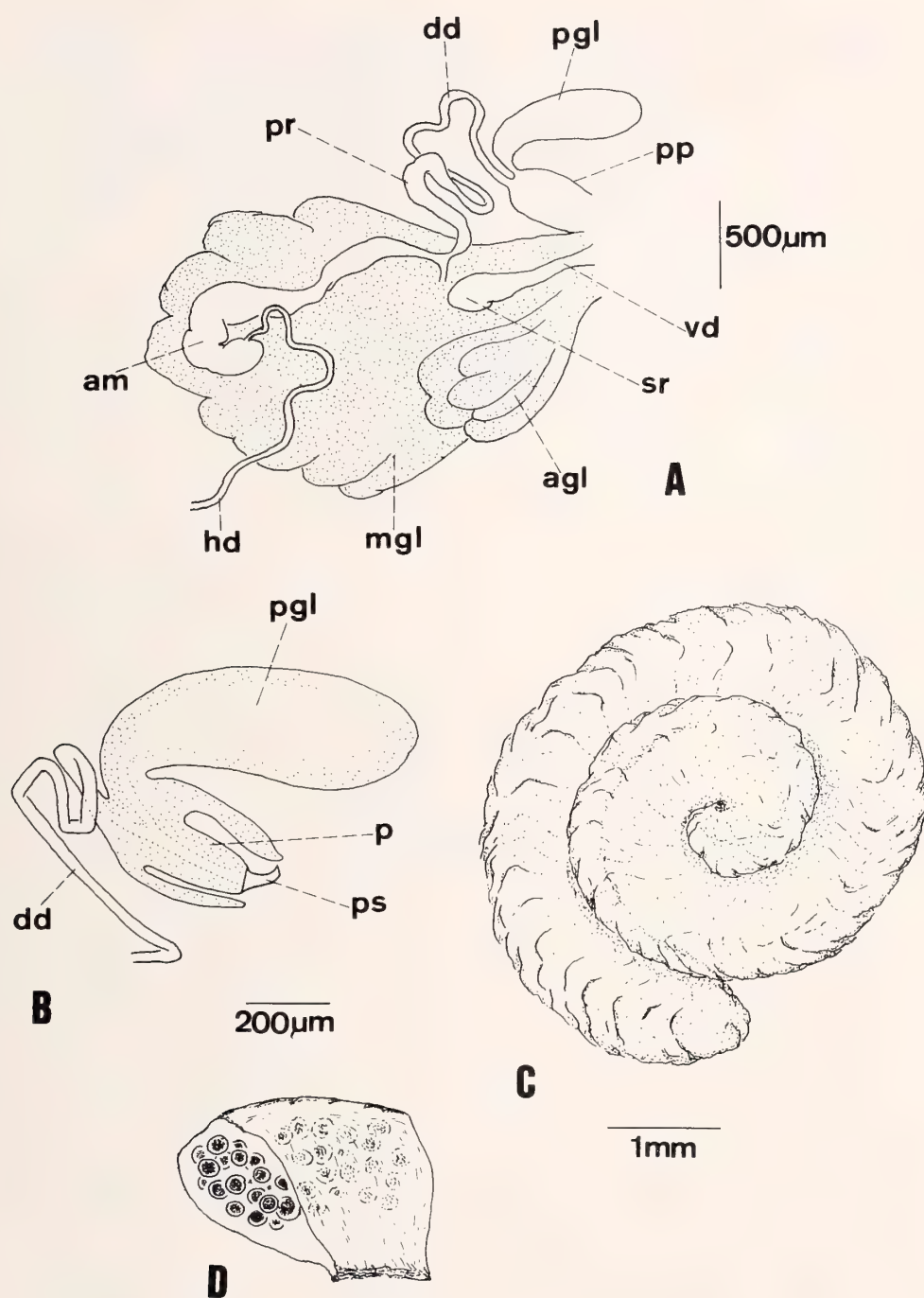


Figure 3

Cuthona willani sp. nov. A. Reproductive system. B. Detail of junction of the penial gland with the penis. C. Spawn. D. Detail of the cross-section of the same. Key: agl, albumen gland; am, ampulla; dd, deferent duct; hd, hermaphroditic duct; mgl, mucous gland; pgl, penial gland; pp, penial papilla; pr, prostate; sr, seminal receptacle; vd, vaginal duct.

Table 1
Comparison of some features of the Lusitanian, Mediterranean, and Mauretanian species of *Cuthona*.

Species	Radular teeth	Lateral denticles	Pre-cardial rows of cerata	Post-cardial rows of cerata	Ceratal shape	Swelling in rhinophores and oral tentacles	Spawn	References†
<i>Cuthona caerulea</i> (Montagu, 1804)	65-80	5-7	5	6	spindle-shaped	no	small ribbon curling anticlockwise	PF (1954); B (1980); Ba (1980); FO (1981); S & P (1982); T & B (1984); T (1988)
<i>C. foliata</i> (Forbes & Goodair, 1839)	51-65	4-7	4-5	4	spindle-shaped	no	broad semicircular coil	B (1980); S & P (1982); T & B (1984); T (1988)
<i>C. viridis</i> (Forbes, 1840)	35-54	5-6	4-5	4-5	cylindrical (more bulbous in juveniles)	no	small opened coil (one turn and a half)	B (1980); T & B (1984); J & E (1985); T (1988)
<i>C. nana</i> (Alder & Hancock, 1842)	≤30	5	12-14		club-shaped	no	(2) broad semicircular coil, convoluted spirally	A & H (1842) (2); PF (1954); B (1980); T & B (1984); T (1988)
<i>C. concinna</i> (Alder & Hancock, 1843)	25-45	4-5	3-4	6-7	clavate	no	?	PF (1954); B (1980); T & B (1984); T (1988)
<i>C. amoena</i> (Alder & Hancock, 1845)	15-20	5	3-4	5-7	clavate	no	small spiral	PF (1954); B (1980); T & B (1984); T (1988)
<i>C. pustulata</i> (Alder & Hancock, 1854)	15-24	4-7	6	6	club-shaped (may be swollen distally)	no	small coil	B (1980); T & B (1984); J & E (1985); T (1988)

Table 1
Continued.

Species	Radular teeth	Lateral denticles	Pre- cardial rows of cerata	Post- cardial rows of cerata	Ceratal shape	Swelling in rhino- phores and oral tentacles	Spawn	References†
<i>C. genovae</i> (O'Donoghue, 1926)	46-57	3-9	1-2	2-3	spindle-shaped	no	coil of one turn	B (1980); S & P (1982); T & B (1984); T (1988)
<i>C. granosa</i> (Schmekel, 1966)	32-34	4-9	2	6	club-shaped	no	ellipsoid/kidney-shaped	S (1966); Sc (1969); S & P (1982)
<i>C. ocellata</i> (Schmekel, 1966)	21	11-14	4	8	club-shaped (apically wider than at the base, rounded above)	no	coil of several turns, wound around the stem of hydroids	S (1966); S & P (1982); Ba (1986)
<i>C. albopunctata</i> (Schmekel, 1968)	58	4	3	4	clavate	no	kidney-shaped/semicircular	S (1968); S & P (1982)
<i>C. ilonae</i> (Schmekel, 1968)	18	6-7	3	3	spindle-shaped (tapering towards the tip)	no	coil of one turn	FO (1981); S (1968); S & P (1982)
<i>C. miniostrata</i> (Schmekel, 1968)	40	3-5	2	5	club-shaped	no	ellipsoid/kidney-shaped	S (1968); S & P (1982)
<i>C. rubescens</i> Picton & Brown, 1978	16-18	8-17	2	9	spindle-shaped with a blunt tip	no	thin, irregularly coiled thread (resembling closely that of <i>C. amoena</i>)	Pi & B (1978); B (1980); T & B (1984); T (1988)
<i>C. thompsoni</i> García, López-González & García-Gómez, 1991	22	14-15	4	6	cylindrical	no	?	G, LG & GG (1991)
<i>C. willani</i> sp. nov.	22	8-10	4	9	urn-shaped and slightly knobly	yes	cup-shaped coil of 2-3 turns	present study

† A & H, Alder & Hancock; B, Brown; Ba, Ballesteros; FO, Fernández-Ovies; G, LG & GG, García, López-González & García-Gómez; J & E, Just & Edmunds; PF, Pruvot-Fol; Pi & B, Picton & Brown; S, Schmckel; S & P, Schmckel & Portmann; Sc, Schönenberger; T, Thompson; T & B, Thompson & Brown.

The ground color of the body is hyaline yellowish white. The body exhibits a very delicate yellow pigmentation and, overlying it, another one of garnet color, less dense than the first. Iridescent red patches are present in some regions of the body, principally on the sides of the head and the right side of the pericardial zone. The oral tentacles have the same ground color as the body from base to the swelling, which has an internal red (violet in the 3-mm specimen) ring. From this level up to the tip, the yellow color is present but the garnet becomes less intense (Figure 1A, B). The rhinophores have a coloration similar to that of the oral tentacles. They exhibit some iridescent red patches at their base, and the enlargements also have an internal red (violet in the 3-mm specimen) ring. From this point up to the tip, the garnet color becomes less intense. The surface of the cerata has a yellow internal pigmentation and a red superficial pigmentation, which becomes denser at both ends of the bigger ceratal enlargements, forming two rings of this color. The yellow pigmentation becomes denser from the upper ring towards the ceratal tip, whereas the red becomes fainter. The ground color of the digestive gland is brown, but at the ceratal base it darkens to reddish brown. The garnet pigmentation is rather violet in the 3-mm specimen. This specimen lacks the lateral patches observed in the remaining specimens, and the tips of the cerata also lack red or violet pigmentation (Figure 1C, E). The preserved specimens conserve the color of the internal rings of the rhinophores and oral tentacles, as well as the dark color of the digestive gland at the base of the cerata.

The broad jaws of the 3-mm and 11-mm paratypes have a delicately denticulated masticatory border (Figure 2B, C). The radular formula of the two paratypes is $21 \times 0.1.0$ and $22 \times 0.1.0$, respectively. The teeth are horseshoe-shaped with a prominent and strong central cusp; the teeth have 8–10 narrow denticles on either side of them in the larger specimen (Figure 2D, E) but only 5 or 6 denticles in the smaller. The larger specimen has 6 teeth with a bifid central cusp (Figures 2D[b], E).

The reproductive system of the 11-mm paratype is illustrated in Figure 3A. The long ampulla is U-shaped. The prostate is curved, and the deferent duct is thin and relatively long; the penis terminates in a penial spine (Figure 3B). There is an ovoid penial gland (Figure 3A, B). The seminal receptacle is elongate, with an enlarged duct that connects with the mucous gland near the genital pore. The nacreous albumen gland also connects with the mucous gland near the genital pore.

Biology: Three egg masses were laid in the laboratory by the El Portil specimens (September 1986). These consisted of 2–3 whorls that formed a cup (Figure 3C). They were triangular in section (Figure 3D) and their surfaces were rough. The width of the string was about 1 mm. Each capsule contained one spherical, white egg. The diameter of the capsules was 136.5–165.7 μm and that of the eggs was 97.5–117 μm .

Discussion: Our specimens are assigned to the genus *Cuthona* Alder & Hancock, 1855, on the basis of their jaws and radulae, despite the similarity in ceratal shape to that of many species of the genus *Eubranhus* Forbes, 1838.

Cuthona caerulea (Montagu, 1804) is the only known species from Lusitanian, Mediterranean, and Mauretanian waters with red ceratal bands. However, despite the high degree of variability of the color pattern of *C. caerulea* (PRUVOT-FOL, 1954; BROWN, 1980; SCHMEKEL & PORTMANN, 1982; THOMPSON & BROWN, 1984; THOMPSON, 1988; CATTANEO-VIETTI *et al.*, 1990), our specimens cannot be considered as specimens of this species because *C. caerulea* lacks the superficial garnet pigmentation, the iridescent red patches present in some regions of the body, and the red-violet internal ring of the swellings of the oral tentacles and rhinophores. Moreover, the cerata of *C. caerulea* are spindle-shaped, not urn-shaped and slightly knobbly, and the oral tentacles and rhinophores have no swellings. Other external and internal differences between *C. caerulea* and *C. willani* are presented in Table 1.

Etymology: The specific name *willani* is chosen to give recognition to our colleague Dr. R. C. Willan from the University of Queensland (Australia) for his excellent contributions to the knowledge of opisthobranch mollusks.

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Two New Species of *Helminthoglypta* (Gastropoda: Pulmonata) from Southern California, with Comments on the Subgenus *Charodotes* Pilsbry

by

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Abstract. Two new species of helminthoglyptid land snails, formerly regarded as outlying populations of *Helminthoglypta traskii* (Newcomb), are described: *Helminthoglypta* (*Charodotes*) *uvasana* from along Grapevine Creek, near Fort Tejon, San Emigdio Mountains, Kern County, and *H.* (*C.*) *vasquezi* from Vasquez Rocks and Agua Dulce Canyon, Los Angeles County, California. Early records of *H. traskii* from Fort Tejon refer to *H. uvasana*. *Helminthoglypta tejonis* Berry, recently considered a subspecies of *H. traskii*, is restored to species rank. The subgenus *Charodotes* Pilsbry is redefined and removed from the synonymy of *Helminthoglypta*, *sensu stricto*. A preliminary list of taxa included in *Charodotes* is presented.

INTRODUCTION

In recent years it has become apparent that the land snail species *Helminthoglypta traskii* (Newcomb, 1861) as construed by virtually all authors (*e.g.*, BARTSCH, 1916; PILSBRY, 1939; ROTH, 1973) is a composite taxon. Several of the taxa that PILSBRY (1939), the last reviser of the genus, regarded as subspecies or populations of *H. traskii* are as distinct anatomically and conchologically as other, recognized, valid species of *Helminthoglypta*.

Helminthoglypta traskii is the type species of the subgenus *Charodotes* Pilsbry, 1939. MILLER (1981, 1985) showed that *Charodotes* was founded on a misconception about the reproductive system of *H. traskii*. PILSBRY (1939) originally had reported that in *Charodotes* the wall of the upper chamber of the penis was single, rather than double as in all other species of *Helminthoglypta*. However, in *H. traskii* and all other species that have been dissected, a double wall is present. As a consequence, *Charodotes* is currently regarded as a synonym of *Helminthoglypta*, *sensu stricto* (*e.g.*, ROTH, 1987).

In this paper we redefine the available name *Charodotes* on the basis of shell and genital characters, remove it from the synonymy of *Helminthoglypta*, *sensu stricto*, and apply it to the clade consisting of the taxa formerly included in *H. traskii*, along with other related species.

Land snails identified as *Helminthoglypta traskii* have been reported from the vicinity of Fort Tejon, Kern County, California, since the early days of biological and geological reconnaissance in the West (NEWCOMB, 1865; COOPER, 1869; BARTSCH, 1916; HANNA, 1927; PILSBRY, 1939). HANNA (1927) examined specimens collected by E. C. Van Dyke in 1927 "on the margin of a wet meadow about a quarter of a mile south of old Fort Tejon" but could find no difference between them and *H. traskii* from the Los Angeles area, except for slightly smaller size. PILSBRY (1939:172–174, fig. 85f) illustrated a specimen collected by the geologist W. M. Gabb at Fort Tejon, and commented that the sculpture was typical for the species.

Fort Tejon is about 3 km southeast of the type locality of *Helminthoglypta tejonis* Berry, 1938 ("two miles above Grapevine Station, old State Highway, Tejon Pass, Kern County"). PILSBRY (1939) regarded *H. tejonis* as a subspecies of *H. traskii*. The circumstance of apparently typical *H. traskii* being found within a few kilometers of the large, distinctive *H. "traskii" tejonis* went unremarked by all later authors.

In March 1987 we collected *Helminthoglypta* along Grapevine Creek immediately north of the north boundary of Fort Tejon State Historical Park, including living adult material for dissection. Comparisons with *H. traskii traskii* and *H. tejonis* (which we will argue herein should be

Table 1
Characters of the subgenera of *Helminthoglypta*.

Character	Subgenus			
	<i>Helminthoglypta</i> , <i>sensu stricto</i>	<i>Charodotes</i>	<i>Rothelix</i>	<i>Coyote</i>
Shell sculpture	various combinations of malleations, spiral striae, and collabral rugae more or less beaded by oblique, divaricating sulci	incised spiral striae, collabral rugae, and papillation of variable strength and distribution	wrinkle-like collabral rugae and dense overall papillation; spiral sculpture generally faint	varying degrees of papillation; spiral striation present in some species
Vagina	opening into atrium near insertion of atrial sac	opening into atrium near insertion of atrial sac	opening into atrial sac near posterior end	opening into atrium near insertion of atrial sac
Lower chamber of penis	short, with small papilla or verge at summit in some species	short, with conic or cylindrical verge at summit in some species	large, sausage-shaped, with post-medial constriction; verge absent	short, more or less cylindrical, with short, broad papilla at summit
Upper chamber of penis	long, slender, club-shaped, cylindrical, or inflated	long, slender, more or less cylindrical; sometimes with swollen anterior portion	short, slender, cylindrical or narrower at anterior end	moderately long, more or less conical, expanding to prominent swelling at lower end

restored to species rank) show that the Grapevine Creek taxon is a new species and it is described below as *Helminthoglypta uvasana*, sp. nov.

Another outlying charodotean *Helminthoglypta* occurs at Vasquez Rocks and in Agua Dulce Canyon, northern Los Angeles County. PILSBRY (1939:fig. 85e) illustrated a specimen from Vasquez Rocks. GREGG (1948:3) referred to it as "a desert modification of *H. traski* [sic]" and considered it subspecifically distinct. Wendell O. Gregg and Walter B. Miller collected it alive at both localities during the 1950s and 1960s. We secured additional living material at Vasquez Rocks in 1988. The species is described below as *Helminthoglypta vasquezi*, sp. nov.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, senior author's collection, San Francisco, California; CAS, California Academy of Sciences; LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History; UCMP, University of California (Berkeley) Museum of Paleontology; USNM, U.S. National Museum of Natural History.

SYSTEMATICS

Family HELMINTHOGLYPTIDAE Pilsbry, 1939

Helminthoglypta Ancey, 1887

Type species: *Helix tudiculata* A. Binney, 1843, by original designation.

(*Charodotes*) Pilsbry, 1939

Type species: *Helix traskii* Newcomb, 1861, by original designation.

Diagnosis: Shell umbilicate, subglobose to depressed, sculptured with incised spiral striae, more or less prominent collabral rugae, and papillation of variable strength and distribution; upper chamber of penis long (double-walled as usual in the genus), slender, more or less cylindrical, with swollen anterior portion in some species; lower chamber of penis simple-walled, short, sometimes with conic or cylindrical verge at summit; vagina opening into atrium near insertion of atrial sac.

Remarks: Table 1 summarizes the diagnostic morphological characteristics of the subgenera of *Helminthoglypta*.

Malleated sculpture, characteristic of the "*Helminthoglypta tudiculata* series" and "*Helminthoglypta nickliniana* series" (PILSBRY, 1939) (groups within the subgenus *Helminthoglypta, sensu stricto*), is absent, or at most weak and localized, in species of *Charodotes*. A clothlike pattern formed by strong collabral rugae cut into beads or granules by oblique, divaricating sulci, found in many species of the *H. nickliniana* series, is unknown in *Charodotes*.

The subgenus *Rothelix* Miller, 1985, has a relatively short and narrow upper penial chamber, a large sausage-shaped lower chamber with a post-medial constriction, and a vagina that opens into the atrial sac near its posterior end. In the subgenus *Coyote* Reeder & Roth, 1988, the upper chamber of the penis is more or less conical, tapering

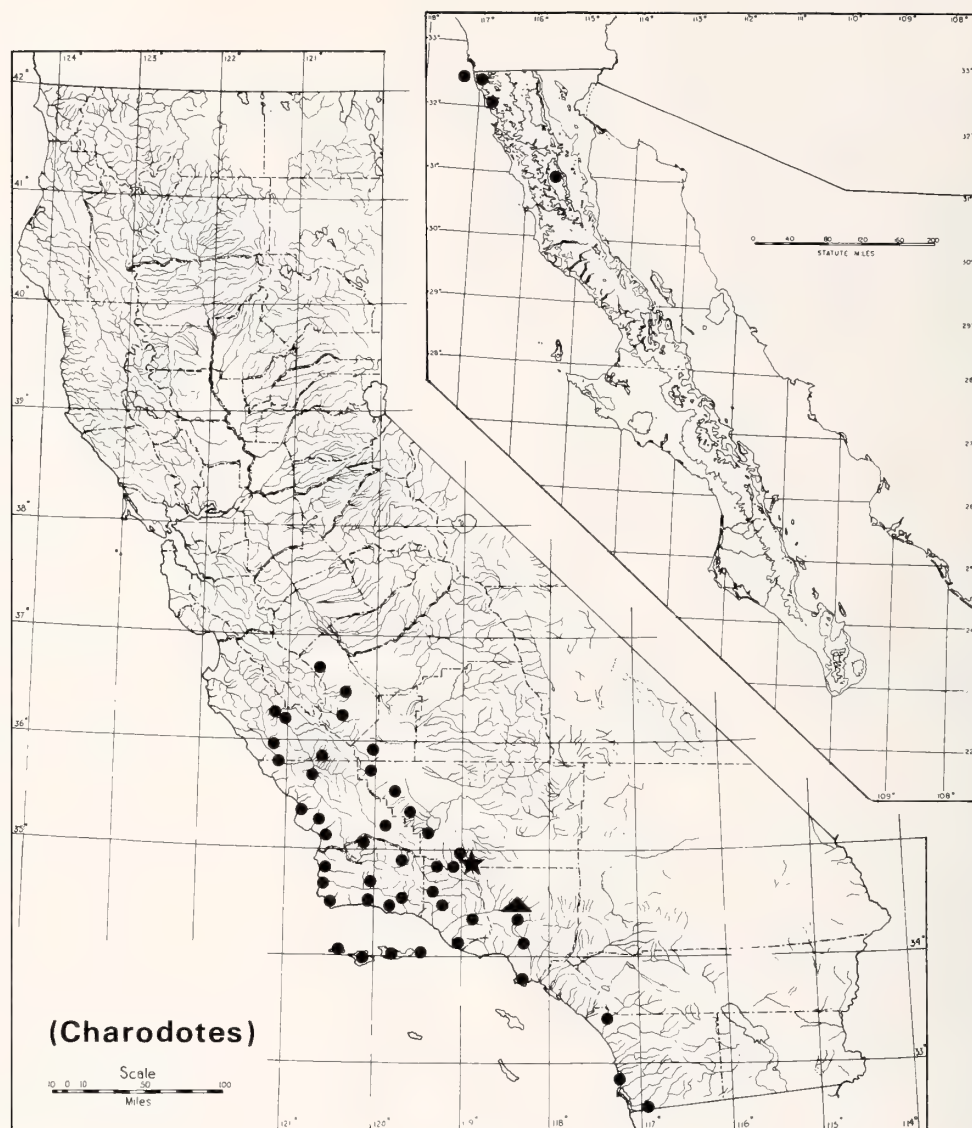


Figure 1

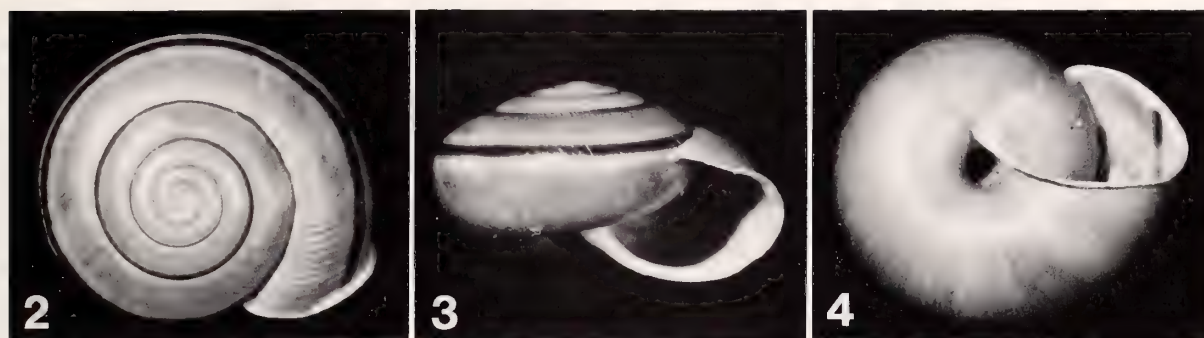
Map of California and (inset) Baja California showing distribution of the subgenus *Charodotes* and type localities of the two new species. Star = type locality of *Helminthoglypta uvasana*. Triangle = type locality of *Helminthoglypta vasquezi*.

from a slender summit to a prominent swelling at the lower end. The swelling is caused by a pronounced thickening of the walls of the inner tube, usually accompanied by enlarged glandular pilasters along the widening lumen. The swelling projects into the lower chamber of the penis in the form of a short, broad papilla. The swollen anterior portion of the upper chamber that occasionally occurs in *Charodotes* (e.g., in *Helminthoglypta sanctaerucis*) consists of a sudden widening, involving both inner and outer walls, and is not homologous with the swelling in *Coyote*.

PILSBRY (1939:68, 170) originally distinguished *Charodotes* from *Helminthoglypta*, *sensu stricto*, mainly on the

basis of a purported single, thick wall of the upper chamber of the penis. However, *H. traskii*, like all other species of *Helminthoglypta*, actually has a double-walled upper chamber (MILLER, 1981, 1985). PILSBRY (1939) also mentioned a common duct of the mucus glands as long as the dart sac or shorter, but as MILLER (1985) noted, this character is variable within populations. *Charodotes* is here redefined primarily on the basis of its striae and papillose shell sculpture and relatively simple, basically cylindrical, upper penial structure.

The following species and subspecies (listed in the order in which they were proposed) are assigned to *Charodotes*:



Explanation of Figures 2 to 4

Figures 2–4. *Helminthoglypta* (*Charodotes*) *uvasana*, sp. nov., shell; holotype SBMNH 35566, top, apertural, and basal views. Diameter 19.8 mm.

Helminthoglypta traskii (Newcomb, 1861)

H. t. traskii

H. t. coronadoensis (Bartsch, 1916)

H. t. isidroensis (Bartsch, 1918)

H. t. pacoimensis Gregg, 1931

H. ayresiana (Newcomb, 1861)

H. carpenteri (Newcomb, 1861)

H. walkeriana (Hemphill, 1911)

H. coelata (Bartsch, 1916)

H. phlyctaena (Bartsch, 1916)

H. willetti (Berry, 1920)

H. sanctaecrucis Pilsbry, 1927

H. fieldi Pilsbry, 1930

H. reediana Willett, 1932

H. misiona Chace, 1937

H. tejoni Berry, 1938

H. reederi Miller, 1981

H. salviae Roth, 1987

H. s. salviae

H. s. mina Roth, 1987

H. uvasana, sp. nov.

H. vasquezii, sp. nov.

Figure 1 depicts the distribution of *Charodotes*, based on these taxa. The following species, which PILSBRY (1939) included in *Charodotes*, may also prove to belong to the subgenus *Helminthoglypta proles* (Hemphill in W. G. Binney, 1892); *H. ferrissi* Pilsbry, 1924; *H. euomphalodes* Berry, 1938; *H. inglesi* Berry, 1938; *H. liodoma* Berry, 1938; *H. stageri* Willett, 1938. *Helminthoglypta hannai* Pilsbry, 1927, from Isla Guadalupe, Baja California, Mexico, may also belong to *Charodotes*. *Helminthoglypta petricola* (Berry, 1916) and its subspecies, included by PILSBRY (1939) in *Charodotes*, belong to the subgenus *Coyote* (REEDER & ROTH, 1988).

In the species here assigned to *Charodotes*, incised spiral sculpture is more prominent than papillation. In *Helminthoglypta avus* (Bartsch, 1916), *Helminthoglypta callistoderma* (Pilsbry, 1917), and *Helminthoglypta orina* Berry, 1938, the penis is cylindrical with a globose swelling at

the lower end of the upper chamber, and papillation is more prominent than incised spiral striae. Pending additional study, we exclude this group of species from *Charodotes*.

Helminthoglypta, *sensu stricto*, as recognized here, is a rather heterogeneous group, which may be subdivided as a result of additional studies now in progress.

Helminthoglypta (*Charodotes*) *uvasana*

Roth & Hochberg, sp. nov.

(Figures 2–5)

Epiphragmophora traskii traskii (Newcomb): BARTSCH, 1916: 613 (in part).

Helminthoglypta traskii (Newcomb): HANNA, 1927:32–34.

Helminthoglypta traski [sic] (Newcomb): PILSBRY, 1939:172–174 (in part), fig. 85f.

Non *Helix traskii* NEWCOMB, 1861:91.

Diagnosis: A medium-sized *Helminthoglypta* with solid, compact, depressed-helicoid, umbilicate shell sculptured with fine spiral striae; granulation present below suture of early whorls, in umbilicus and behind lip; body whorl tightly coiled, scarcely descending.

Description—shell of holotype: Shell (Figures 2–4) of medium size for genus, solid, compact, moderately glossy, depressed-helicoid, umbilicate; umbilicus contained 8.25 times in major diameter. Spire low-conic; whorl profile moderately convex; suture distinctly impressed. Embryonic whorls 1.7, narrower than immediately following teleoconch whorl; nuclear tip smooth, thereafter granulose with low, coarse, irregular collabral rugae and scattered papillae; zone below suture densely granulose. Early teleoconch whorls with low, convex-forward, collabral rugae; minor granulation below suture; sparse and inconspicuous papillation; and, from third whorl on, fine, incised spiral striae. Striae weak and discontinuous at first, becoming stronger and continuous on later whorls. Striae prominent on body whorl, continuing over base into umbilicus. Base moderately inflated, tumid around umbilicus, granulose within

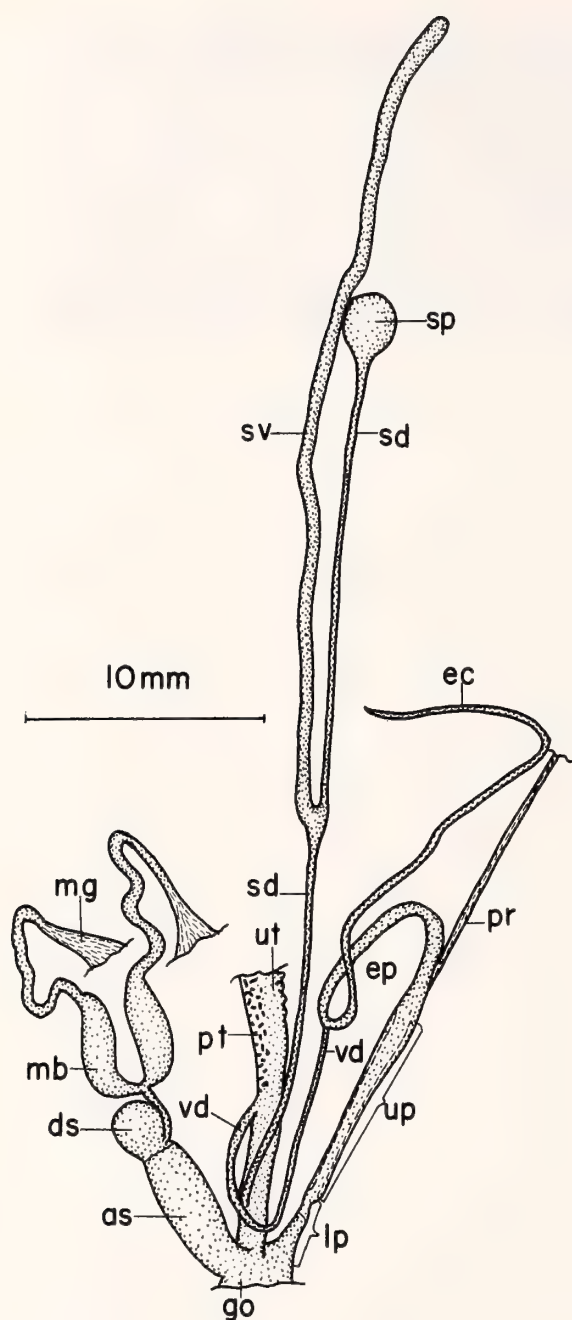


Figure 5.

Helminthoglypta (Charodotes) uvasana, sp. nov., reproductive system, drawn from projection of stained whole mount; ovotestis and albumen gland region omitted; paratype SBMNH 35567. Abbreviations: as, atrial sac; ds, dart sac; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; lp, lower chamber of penis; mb, mucus gland bulbs; mg, part of mucus gland membranes; pr, penial retractor muscle; pt, lower part of prostate; sd, spermathecal duct; sp, spermatheca; sv, spermathecal diverticulum; up, upper chamber of penis; ut, part of uterus; vd, vas deferens.

umbilicus and behind lip. Body whorl tightly coiled, scarcely descending except just before aperture, not constricted behind lip. Aperture auricular, moderately oblique; plane of peristome at angle of 35° to vertical; lip turned outward, narrowly expanded, scarcely reflected except at columellar insertion. Upper limb of peristome produced and slightly downturned. Inner lip weakly encroaching on umbilicus. Parietal callus thin, granulose, with sculpture of parietal wall showing through. Shell pinkish tan under a yellowish brown periostracum; with a 1.0-mm-wide russet spiral band on shoulder (prolonging trajectory of suture) with pale zones of equal width (lower zone more conspicuous) on either side of band. Diameter (exclusive of expanded lip) 19.8 mm, height 11.5 mm, width of umbilicus 2.4 mm, whorls 5.7.

Measurements and counts of material at hand ($n = 38$): Range of adult shell diameter 17.4–23.5 mm. Number of whorls 5.3–6.4; number of embryonic whorls 1.7–2.0. Umbilicus contained 7.5–9.0 times in shell diameter.

Soft anatomy: Mantle over lung clear buff, about 30% covered with irregular black spots. Reproductive system (Figure 5) typical of *Charodotes*. Atrium short and broad. Atrial sac cylindrical, about twice as long as vagina, with spherical dart sac at upper end, lacking a glandular collar. Mucus gland bulbs of moderate size, joined by slender, Y-shaped common duct. Duct of spermatheca slender throughout its length, bearing diverticulum of greater diameter, about 1.5 times as long as spermathecal duct above its origin. Penis with short, conical lower chamber (approximately as long as vagina) and long, double-walled upper chamber, cylindrical or slightly wider at summit, leading to epiphallus of same diameter. Verge absent. Epiphallic caecum about as long as penis plus epiphallus.

Type material: Holotype: Santa Barbara Museum of Natural History, SBMNH 35566 (shell, whole mount of mantle tissue, and stained whole mount of reproductive system), CALIFORNIA: Kern County: along Grapevine Creek in Castaic Valley, immediately north of boundary of Fort Tejon State Historical Park (projected SE $\frac{1}{4}$ sec. 9 to NE $\frac{1}{4}$ sec. 16, T. 9 N, R. 19 W, San Bernardino Base and Meridian), elevation approximately 940 m (3100 ft); under downed log of *Quercus lobata*. W. B. Miller, F. G. Hochberg, B. Roth coll., 9 March 1987.

Paratypes: SBMNH 35567 (10 shells and stained whole mount of reproductive system), from same locality as holotype, under downed oak logs in leaf litter, in brush, and in wood rat nests. Additional paratypes deposited in ANSP, CAS, BR, LACM, and USNM.

Referred material: CALIFORNIA: Kern County: Fort Tejon (ANSP 10697, BR 448, CAS 036312, CAS 051338, UCMP 2497, USNM 58523); near Old Fort Tejon (BR 774, BR 1539, CAS 036330); "Tejon" [*sic*] (ANSP 10698, W. M. Gabb coll., one specimen figured by PILSBRY, 1939: fig. 85f); Grapevine Creek at Fort Tejon (SBMNH 35568);



Explanation of Figures 6 to 8

Figures 6–8. *Helminthoglypta tejonis* Berry, shell; holotype SBMNH 34216, top, apertural, and basal views. Diameter 30.3 mm.

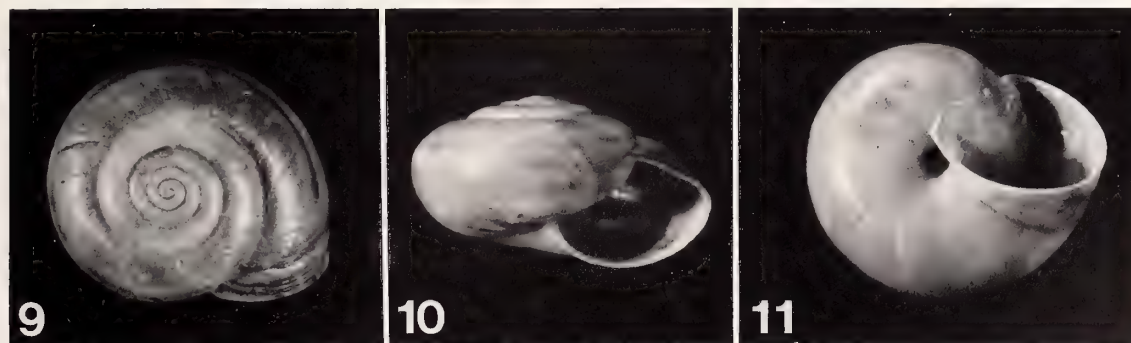
Grapevine Canyon, 0.25 mi [0.4 km] S of Old Fort Tejon (CAS 036290); 0.5 mi [0.8 km] N of Tejon Inn (LACM 114626). Los Angeles County: Oak Flat Ranger Station, 12 mi [19 km] N of Castaic (CAS 036300).

Remarks: *Helminthoglypta uvasana* somewhat resembles presumed topotypic *Helminthoglypta traskii traskii* from Point Fermin, Los Angeles County. The shells of both species are robust and run through about the same range of size and shape, but the incised spiral sculpture of *H. uvasana* is finer (7 striae/mm on the last $\frac{1}{4}$ of the body whorl, compared to 4–5 striae/mm at the same location on *H. traskii*). In *H. traskii* the spermathecal diverticulum is 1.5–2 times as long as the spermathecal duct above its origin. The lower chamber of the penis is longer than that of *H. uvasana*.

Helminthoglypta uvasana differs from *H. carpenteri* of the southwestern San Joaquin Valley in having a black-spotted mantle when adult. In *H. carpenteri* the mantle over the lung is uniform brownish gray with a black transverse line behind the mantle collar; small juveniles some-

times have black spots. The base of the spermathecal duct of *H. carpenteri* is cavernous; the spermathecal diverticulum is only slightly longer than the spermathecal duct above its origin. The collabral rugae on the shell of *H. carpenteri* are more or less granulose.

Helminthoglypta tejonis occurs approximately 3 km to the northwest (the type locality probably is in the projected SE $\frac{1}{4}$ of sec. 32, T. 10 N, R. 19 W), and about 21 km west of that, along San Emigdio Creek. The shell of *H. tejonis* (Figures 6–8) is larger (26.0–31.2 mm in diameter), thin, broadly depressed-helicoid, with 6.25–7.25 whorls. The spire is broadly conic to low-domed, the suture impressed, the whorls shouldered and somewhat flattened. The periphery is broadly rounded, sloping toward the base. Incised spiral striae first appear on the fourth whorl. Papillation is faint to obsolete, confined to the early neanic whorls, and sometimes replaced by minute pits on later whorls. The umbilicus is contained 9–10 times in the shell diameter, about $\frac{1}{4}$ covered by the inner lip. The base of the embryonic whorls is visible in the umbilicus, centered within a regular spiral; in *H. uvasana* the pit of the um-



Explanation of Figures 9 to 11

Figures 9–11. *Helminthoglypta vasquezii*, sp. nov., shell; holotype SBMNH 35569, top, apertural, and basal views. Diameter 16.4 mm.

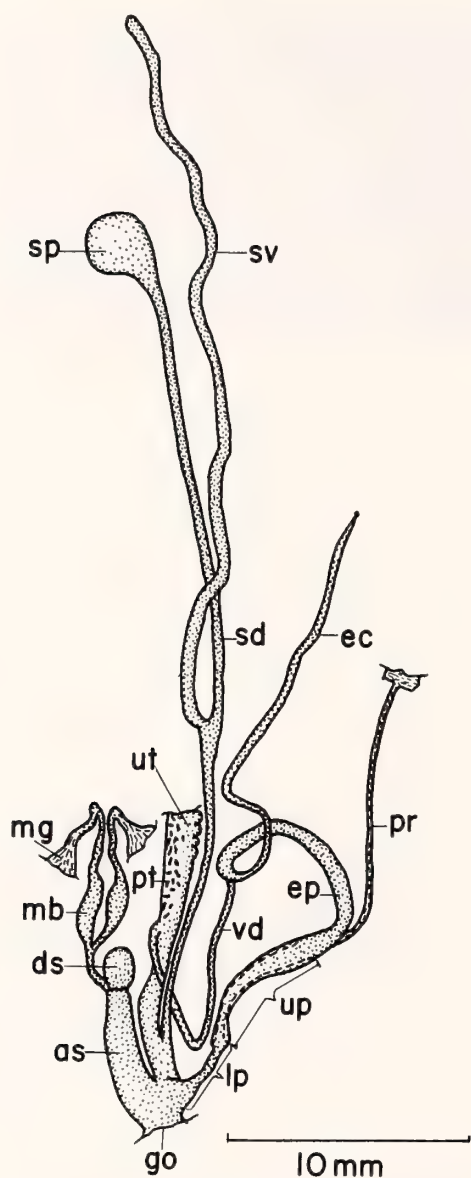


Figure 12

Helminthoglypta vasquezi, sp. nov., reproductive system, drawn from projection of stained whole mount; paratype SBMNH 35570. Abbreviations as in Figure 5.

bilicus is oblique and the embryonic whorls are not readily visible. The spermathecal diverticulum in *H. tejonis* is about as long as the spermathecal duct above its origin. The lower chamber of the penis is rather broadly cylindrical and approximately twice as long as the vagina; its upper half is nearly filled by a thick, cylindrical verge.

Helminthoglypta tejonis has (in common with *H. phlyctaena* and *H. willetti*) a glossy, tumid, broadly depressed-helicoid shell generally more than 25 mm in diameter; the spiral striae are mostly shallow, and papillation is confined

to the early neanic whorls. In *H. traskii* the shell is matte to moderately glossy and rarely exceeds 24 mm in diameter. The spiral striae are coarse and strongly impressed. In subspecies *H. traskii pacoimensis* and *H. traskii isidroensis*, papillation extends onto the body whorl; in *H. t. traskii*, papillation fades out by the third or fourth whorl. The spermathecal diverticulum in *H. traskii* is 1.5–2 times as long as the spermathecal duct above its origin. The lower chamber of the penis is cylindrical, relatively long (up to twice as long as the vagina), and sometimes slightly flaring at the base. A verge is absent.

The shell and reproductive system distinctions cited above (especially the presence of a verge in *Helminthoglypta tejonis* and not in *H. traskii*) lead us to restore *H. tejonis* to species rank, as originally proposed for it by BERRY (1938).

The natural vegetation of the San Emigdio Mountains in the vicinity of Fort Tejon is valley oak (*Quercus lobata*) savanna, grading locally to chaparral (KÜCHLER, 1977). Along Grapevine Creek we found the new species under logs and leaf litter among *Quercus lobata*, nettle (*Urtica holoserica*), and poison-oak (*Rhus diversiloba*).

Etymology: Latin, *uvasana*, pertaining to Canada de las Uvas, a former name for Grapevine Creek (cf. BREWER, 1930). The name "grapevine shoulderband" is proposed for purposes of the American Fisheries Society list of the common names of mollusks (see TURGEON et al., 1988) and other administrative uses.

Helminthoglypta (*Charodotes*) *vasquezi*,
Roth & Hochberg, sp. nov.

(Figures 9–12)

Helminthoglypta traski [sic] (Newcomb): PILSBRY, 1939:172–174 (in part), fig. 85e.

Non *Helix traskii* NEWCOMB, 1861:91.

Diagnosis: A small *Helminthoglypta* with thin, delicate, depressed, narrowly umbilicate shell, with fine spiral striae first appearing on last 1/4 of penult; body whorl flaring behind lip, scarcely descending.

Description—shell of holotype: Shell (Figures 9–11) small for genus, thin and delicate, moderately glossy, depressed, umbilicate; umbilicus contained 10.0 times in major diameter. Spire scarcely elevated, low-domed; whorl profile moderately flattened; suture impressed. Embryonic whorls 1.6; nuclear tip smooth, thereafter granulose with low, coarse, irregular collabral rugae and scattered papillae. Early teleoconch whorls with fine, overall, radial wrinkling and crude, convex-forward, collabral rugae, strongest below suture. From third whorl on, minute, more or less diagonally arranged papillation superimposed, fading out on body whorl except for few scattered papillae. Fine, incised spiral striation first appearing on last 1/4 of penult, more prominent on body whorl, continuing over base into umbilicus. Base rather deep, tumid around umbilicus, granulose within umbilicus and behind lip. Body whorl

expanding rapidly, flared behind lip, scarcely descending except just before aperture, not constricted behind lip. Aperture ovate, moderately oblique; plane of peristome shallowly sinuous in profile, at angle of 45° to vertical; lip thickened but not markedly turned outward, reflected only below columellar insertion. Upper limb of peristome produced and slightly downturned. Inner lip weakly encroaching on umbilicus. Parietal callus very thin, granulose, with sculpture of parietal wall showing through. Shell translucent, pale pinkish tan under a yellowish olive periostracum; with a 0.5-mm-wide russet spiral band on shoulder (prolonging trajectory of suture), indistinctly bordered by pale zones (upper zone 0.5 mm wide, lower zone 1.0 mm wide). Diameter (exclusive of expanded lip) 16.4 mm, height 9.4 mm, width of umbilicus 1.6 mm, whorls 5.4.

Measurements and counts of material at hand ($n = 66$): Range of adult shell diameter 14.6–19.0 mm. Number of whorls 4.5–5.4; number of embryonic whorls 1.4–1.9. Umbilicus contained 7.5–10.0 times in shell diameter.

Soft anatomy: Mantle over the lung clear buff with black maculation. Reproductive system (Figure 12) typical of *Charodotes*. Atrium short and broad. Atrial sac cylindrical-conic, approximately twice as long as vagina, with a spherical dart sac at upper end, lacking a glandular collar. Mucus gland bulbs rather small, joined by Y-shaped common duct. Duct of the spermatheca slender throughout its length, bearing a diverticulum of greater diameter, about 1.25 times as long as spermathecal duct above its origin. Lower chamber of penis short (slightly longer than vagina), narrowly cylindrical, and flaring at base. Double-walled upper chamber moderately long, widening slightly toward summit, leading to epiphallus of same diameter. Verge absent. Epiphallallic caecum about as long as penis plus epiphallus.

Type material: Holotype: Santa Barbara Museum of Natural History, SBMNH 35569 (shell, whole mount of mantle tissue, and stained whole mount of reproductive system), CALIFORNIA: Los Angeles County: Vasquez Rocks County Park, in small, north-facing amphitheater south of road, west of most prominent outcrops (NE¼ SW¼ sec. 26, T. 5 N, R. 14 W, San Bernardino Base and Meridian); under clump of *Yucca whipplei*. W. B. Miller, J. D. Goodman, F. G. Hochberg, B. Roth coll., 12 February 1988.

Paratypes: SBMNH 35570 (12 shells and stained whole mount of reproductive system), from same locality as holotype. Additional paratypes deposited in ANSP, BR, CAS, LACM, and USNM.

Referred material: CALIFORNIA: Los Angeles County: Vasquez Rocks (BR 781, CAS 036791, CAS 036792, CAS 036795, LACM 65520, LACM 114608, SBMNH 35571, SBMNH 35572, SBMNH 35573, SBMNH 35574); Vasquez Rocks, off Mint Canyon highway, west end about 3 mi [4.8 km] south of highway under roots of yucca (ANSP 157180, one specimen figured by PILSBRY, 1939:fig. 85e);

ridge on N side of Escondido Canyon, Vasquez Rocks County Park, in *Yucca whipplei* clumps (BR 1611); Agua Dulce Canyon 1.5–2.1 mi [2.4–3.4 km] from junction with Soledad Canyon (SBMNH 35575, SBMNH 35576, SBMNH 35577, SBMNH 35578, SBMNH 35579, SBMNH 35580, SBMNH 35581, SBMNH 35582).

Remarks: *Helminthoglypta vasquezii* differs from *H. traskii* and *H. uvasana* in that the shell is thin and delicate with fine spiral striation that does not appear until the last part of the penultimate whorl. The striation in *H. traskii* is coarser and present by the third whorl. The umbilicus of *H. traskii* is contained 10–12 times in the shell diameter. The spermathecal diverticulum in *H. traskii* is 1.5–2 times as long as the spermathecal duct above its origin.

Helminthoglypta vasquezii resembles *H. salviae* from the vicinity of Frazier Park, Kern County, and Quatal and Apache canyons, Ventura County, in having a depressed shell with spire scarcely elevated and a pit-like umbilicus less than one-third covered by the inner lip. The shell of *H. salviae* is thin but not especially delicate; the collabral rugae are smooth or partly broken up into rows of granules; and the body whorl is tightly coiled throughout, rather than rapidly expanding and flaring behind the aperture as in *H. vasquezii*.

The natural vegetation at the type locality is semi-desert chaparral, including *Adenostoma fasciculatum*, *Juniperus californica*, and extensive patches of *Yucca whipplei*.

Etymology: The species is named for the outlaw and folk hero Tiburcio Vasquez (born 1835, hanged 1875), who plied his trade in the Vasquez Rocks area during the 1870s. The name “Vasquez shoulderband” is proposed for purposes of the American Fisheries Society list of the common names of mollusks (see TURGEON *et al.*, 1988) and other administrative uses.

ACKNOWLEDGMENTS

Walt Miller participated in the field work, prepared the whole mounts and drawings of reproductive systems, and discussed helminthoglyptid systematics with us. John D. Goodman assisted with field work and located a population of live adult snails at Vasquez Rocks County Park. Miller and Dick Reeder critically read the manuscript. Gene Coan furnished historical literature. Ken Heartsill provided assistance and information on Fort Tejon State Historical Park. Frank T. Hovore issued a collecting permit and Ranger Mike Sharp assisted in the field at Vasquez Rocks County Park, a North Region Natural Areas Park under the jurisdiction of the Los Angeles County Department of Parks and Recreation.

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Seasonal Variation in the Reproductive Organs of Two Populations of *Caracolus caracolla* (Linné) (Pulmonata: Camaenidae) in Puerto Rico

by

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Abstract. Environmental factors such as temperature, water, and day length may influence the reproductive cycle of pulmonates. To determine if environmental conditions influence the reproductive seasonality of the pulmonate *Caracolus caracolla* (Linné), the histology of the reproductive system from members of two populations was compared. One population of snails was from a rain forest and the other was from a dry coastal plain. Four reproductive organs were studied: the ovotestis, hermaphroditic duct, spermatheca, and albumen gland. The snails were collected monthly and their organs were dissected, measured (size and mass), and sectioned for microscopical examination. Histological and morphological changes indicated seasonal variation in the reproductive organs of *Caracolus caracolla* from both populations. Statistical analyses show a significant difference in almost all of the morphological measurements of the shells and reproductive organs within and between each population. The gametes were fully developed, in both populations, by April and May. It is possible that the snails from both populations are mating continually throughout the year, since spermatozoa were always present in the hermaphroditic duct. Nevertheless, according to the activity of the spermatheca, there are some peaks of mating activity in December for the dry coastal plain population and in February for the rain forest population. The onset of mating was correlated with an increase in precipitation, especially in the rain forest population. These results incorporate changes that occurred during one year. To determine if these changes occur cyclically, the study would need to be extended by several years.

INTRODUCTION

Environmental factors such as temperature (BOUILLON, 1956; WOLDA, 1967; RIDDLE, 1983; TOMPA, 1984), water (RIDDLE, 1983; SOLEM & CHRISTENSEN, 1984; TOMPA, 1984), and day length (HENDERSON & PELLUET, 1960; SOKOLOVE & MCCRONE, 1978; TOMPA, 1984) can regulate some physiological aspects of terrestrial pulmonates. The possible effects of these external factors on the reproductive cycle has not been studied extensively at the histological level. In the present study the annual reproductive cycles of two populations of the terrestrial pulmonate *Caracolus caracolla* (Linné, 1758) were analyzed. The morphology and histology of the reproductive system were studied

throughout the year to determine if the reproductive organs undergo seasonal variation.

Studies on terrestrial pulmonates have revealed a seasonal variation in the morphology of their reproductive organs. SOLEM & CHRISTENSEN (1984) worked with Australian camaenids and concluded that there is a seasonal variation in the reproductive activity of mature adults. They determined reproductive activity by analyzing the seasonal variation of the size of the reproductive organs. HEATWOLE & HEATWOLE (1978) studied the annual cycle of reproduction in the camaenid *Caracolus caracolla* by determining the seasonal occurrence of copulation and oviposition and the temporal changes in weight of the albumen gland. They compared two Puerto Rican populations, one living in a rain forest and the other in a dry coastal area, and observed two different seasonal patterns in the glandular weights of the populations.

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The effect of environmental factors, such as temperature and illumination, on the function of the reproductive organs was studied at the histological level by SMITH (1966). He observed that a "critical point" in the maturation of the reproductive tract of the pulmonate *Arion ater* occurs when spermatozoa from the ovotestis enter the hermaphroditic duct. This critical point acts as a trigger for the maturation of the rest of the tract; no external factor has an effect on subsequent maturation of the organs, even though before this critical point, during spermatogenesis, external factors may have a large effect. He mentioned that a trigger mechanism of control, probably of neurosecretory nature, must be operating in the pulmonate. SMITH (1966) observed that the reproductive systems of slugs that were hatched and reared in the laboratory under temperatures of 18°C, natural illumination, and abundant fresh food matured seven months earlier than the reproductive systems of wild slugs.

The timing of the onset of the breeding season for the pulmonate *Helminthoglypta arrosa* (Binney, 1855) may depend on food and water availability but is not dependent on temperature variations (VAN DER LAAN, 1980). Two studies show that high environmental humidity is essential for oviposition (CARRICK, 1942) and mating (RUNHAM & LARYEA, 1968) in the slug *Agriolimax reticulatus*.

The reproductive tract of terrestrial and freshwater gastropods is under endocrinological control (PELLUET & LANE, 1961; PELLUET, 1964; BOER & JOOSE, 1975; TAKE-DA, 1979). The maturation of oocytes in pulmonates is controlled by a hormone secreted by the dorsal bodies, a structure associated with the cerebral ganglia (GERAERTS & JOOSE, 1975; WIJDENES & RUNHAM, 1976). These endocrinological mechanisms are affected by environmental factors such as photoperiod and humidity (RUNHAM & LARYEA, 1968; SMITH, 1966; SOKOLOVE & MCCRONE, 1978), which have a greater effect on spermatogenesis than on oogenesis.

This study presents the first histological comparison of the reproductive system of the camaenids living under different environmental conditions of temperature and humidity. A pattern of reproductive activity was established for the pulmonate *Caracolus caracolla* and could be used for the study of other pulmonates.

MATERIALS AND METHODS

The endemic terrestrial pulmonate *Caracolus caracolla* (Linné, 1758) is abundant in the forests of the central mountains as well as in the humid lowland forests of Puerto Rico. The shell is large (55–60 mm in diameter), dextrally coiled, and light to dark brown.

Study Sites

Two populations were studied. The El Yunque population lives in a subtropical rain forest (Sierra Palm Forest) located on the Mt. Britton Trail of the Luquillo Experimental Forest, Puerto Rico, at an elevation of about 850

m. The relative humidity of the region is over 90% throughout the year, the temperature fluctuates from 13 to 18°C, and the total annual precipitation is over 2.5 m (HEATWOLE & HEATWOLE, 1978). In 1988, the annual temperature range for El Yunque was from 17 to 20°C, and the total precipitation for the year was 44.95 m (NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION [NOAA], 1989).

The Loiza population lives in a dry coastal plain located at sea level on the northern coast of Puerto Rico. Rainfall in this area is sparser and more seasonal than in the mountains. The annual temperature range for 1988 was from 26 to 29°C, and the total precipitation for the year was 24.3 m (NOAA, 1989).

Collection and Dissection of Specimens

Ten mature specimens from each population were collected monthly for a period of one year beginning in September 1987. The criterion used to determine maturity was the thickness of the lip of the shell (reflected shell lip). A hygrometer was used to measure temperature and relative humidity in the area immediately surrounding the animals each month.

The snails were relaxed by placing them in a freezer (5°C) for about half an hour. After being removed from the freezer, the height and width of the shell were measured. The snails were then placed in a dissecting dish that contained a physiological saline solution of 0.75% NaCl to prevent tissue damage.

Viewed through an Olympus SZ dissecting microscope, the reproductive system was excised with a scalpel through a ventral lengthwise cut on the body wall. The ovotestis, hermaphroditic duct, spermatheca, and the albumen gland (Figure 1) were removed from the tract and measured (length and width) with a vernier caliper. The ovotestis was difficult to remove because it is embedded in the digestive gland. For this reason a scalpel was used to cut the edges of the ovotestis, although parts of the digestive gland remained attached to it. The mass of each organ except the ovotestis was determined by placing it in a separate small petri dish that contained a pre-measured mass of physiological saline and weighed to the nearest 0.001 g using a Sartorius balance, model L420D. The organs were then fixed in Bouin's fluid.

Histological Methods

After fixation, the tissues were dehydrated, cleared in benzene, and embedded in Paraplast. Sections were cut at 10 μ m and stained with Harris' modified hematoxylin (HUMASON, 1979). Some sections of the reproductive organs were stained with Milligan Trichrome (HUMASON, 1979), which stains muscular and connective tissue.

Histological Examination

Sections through different regions of the reproductive organs of each specimen were examined with a light mi-



Figure 1

The reproductive system of the hermaphroditic snail *Caracolus caracolla*. Key: ag, albumen gland; dg, digestive system; ep, epiphallus; go, genital opening; hd, hermaphroditic duct; o, ovotestis; ov, oviduct; p, penis; s, spermatheca; sd, spermathecal duct; v, vagina; vd, vas deferens (scale = 10 mm). Top of the figure is anterior.

croscope. Observations were recorded to compare the histology of the monthly samples and to determine if there were seasonal changes in the activity of these organs.

Germinal cells (oogonia and spermatogonia) at different stages of development and somatic cells were identified in the acini of the ovotestis. The lumen of the seminal vesicles of the hermaphroditic duct and the lumen of the spermatheca were analyzed to determine the presence of spermatozoa, since this is a sign of reproductive activity. The albumen gland was studied only at a morphological level (size and mass) because the active albumen glands are brittle and difficult to section.

Statistical Analysis

The statistical analysis gave a quantitative measure of the successive changes in the reproductive organs during the year. Thirteen measurements were taken from each snail. These included the lengths and widths of the shell and ovotestis and the lengths, widths, and masses of the hermaphroditic duct, spermatheca, and albumen gland. One-way and two-way analyses of variance (ANOVA),

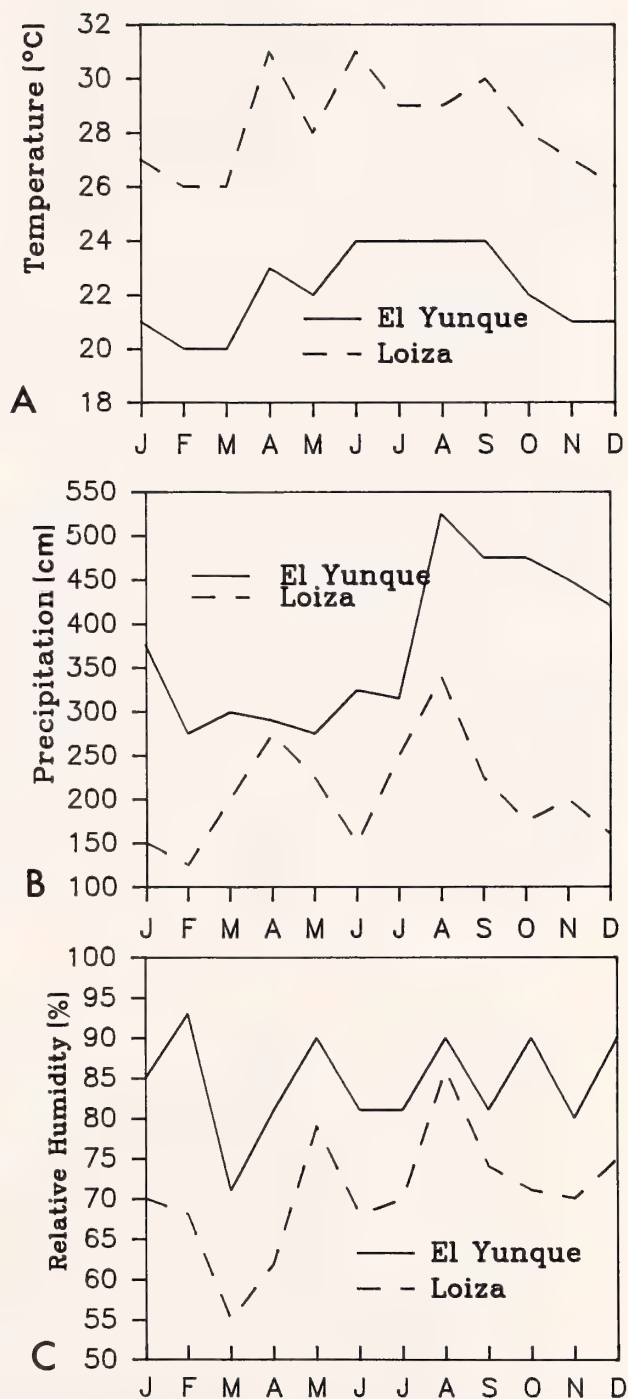


Figure 2

A. Annual (1988) temperature data for El Yunque and Loiza.
 B. Annual (1988) precipitation data for El Yunque and Loiza.
 C. Annual (1988) relative humidity data for El Yunque and Loiza.
 El Yunque (—), Loiza (---).

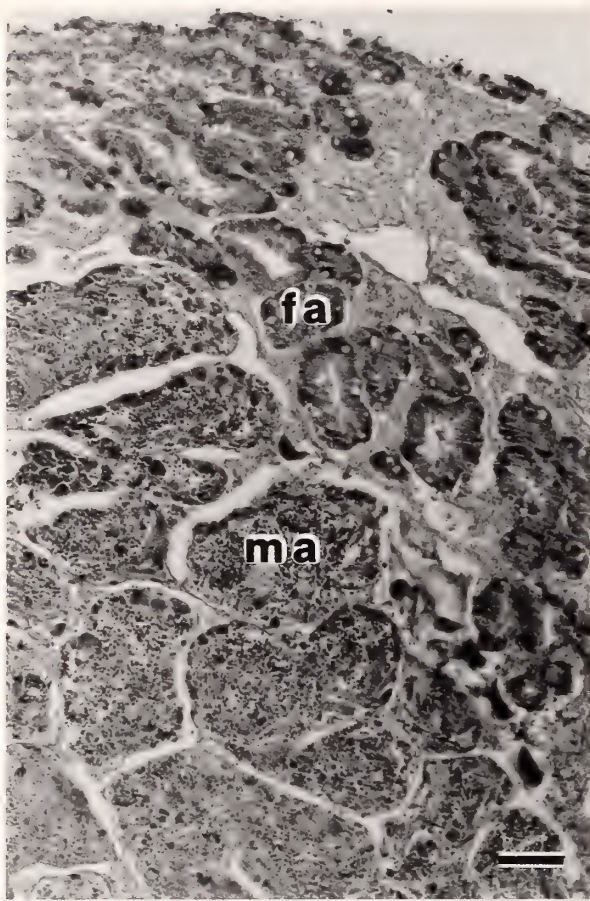


Figure 3

Photomicrograph of separate male (ma) and female (fa) acini. The male acini tended to be located near the center of the ovotestis (scale = 1 mm).

Principal Component analyses, and Pearson Correlation Coefficient comparisons were performed using the SAS program.

RESULTS

Climatological Data

The patterns of monthly precipitation for 1988 were similar for the two sites, but precipitation was consistently greater in El Yunque (Figure 2). Monthly temperatures in 1988 were also similar, but the temperature at El Yunque was always 6–7°C lower than at Loiza. The patterns of relative humidity were similar to the precipitation data. The average annual value for the El Yunque population was 89% and for Loiza 73%.

Morphology and Histology of the Reproductive Organs

Ovotestis: The ovotestis is embedded in the digestive gland and consists of many irregularly shaped acini (Figure 3).

Each acinus is bordered by a layer of cells, the germinal epithelium, and is separated from the other acini by connective tissue. The germinal epithelium is one cell thick and consists of columnar cells with basal nuclei. Separate acini in the ovotestis give rise to spermatozoa and ova (Figures 3, 4A–C).

The process of oogenesis and spermatogenesis begins in the germinal epithelium and ends in the lumen of the acini, where the mature gametes are liberated. The spermatogonia develop into spermatocytes (Figure 4B), which become attached to the Sertoli cells. Mature spermatozoa are released from the Sertoli cells and remain in the lumen until they are carried to the hermaphroditic duct for storage.

The oocytes develop in the wall of the acinus (Figure 4C). During some months of the year, yellowish cells were seen near the developing oocytes. These cells were probably follicular cells that surround the oocyte. A mature oocyte is round; its cytoplasm and nucleus stain very dark (Figure 4C). The lumen of each acinus collects the mature gametes and connects to the hermaphroditic duct via collecting tubules that transport the mature gametes.

Hermaphroditic duct: The hermaphroditic duct has three distinctive parts. The proximal part of the duct to the ovotestis does not store sperm. The next part, the seminal vesicles, have diverticula, which function to store auto-sperm. The distal part of the duct opens into the talon or fertilization pouch, where oocytes are fertilized by allo-sperm. The sections that were analyzed in this study came from the seminal vesicles (Figure 5). About half of the cells comprising the epithelium of the seminal vesicles are ciliated. The ciliated epithelium has narrow cells with basal nuclei and the rest of the epithelium is cuboidal with central nuclei (Figure 6). The vesicles are bordered by circular and longitudinal muscle fibers.

Spermatheca: The spermatheca, or bursa copulatrix, has a large lumen and a wall composed of three layers (Figures 7, 8). The layer that borders the lumen consists of two different types of cells, one of which has microvilli at the apical end. The middle layer consists of longitudinal and circular muscle fibers with some pigment cells in between. The third layer is an epithelium that borders the external wall.

Albumen gland: The albumen gland is the organ that fluctuates the most in size and color. When inactive the organ is beige and short (15 mm long); when active, it is an intense yellow and two or three times larger. The gland is a tubular, bean-shaped organ that consists of branching tubules separated by connective tissue. The walls of the tubules have secretory cells that have basal nuclei and rounded granules during some months of the year. The tubules lead into a number of small ducts, which unite to form a central duct (Figure 9). The central duct is lined by a ciliated epithelium that varies from cuboidal to columnar.

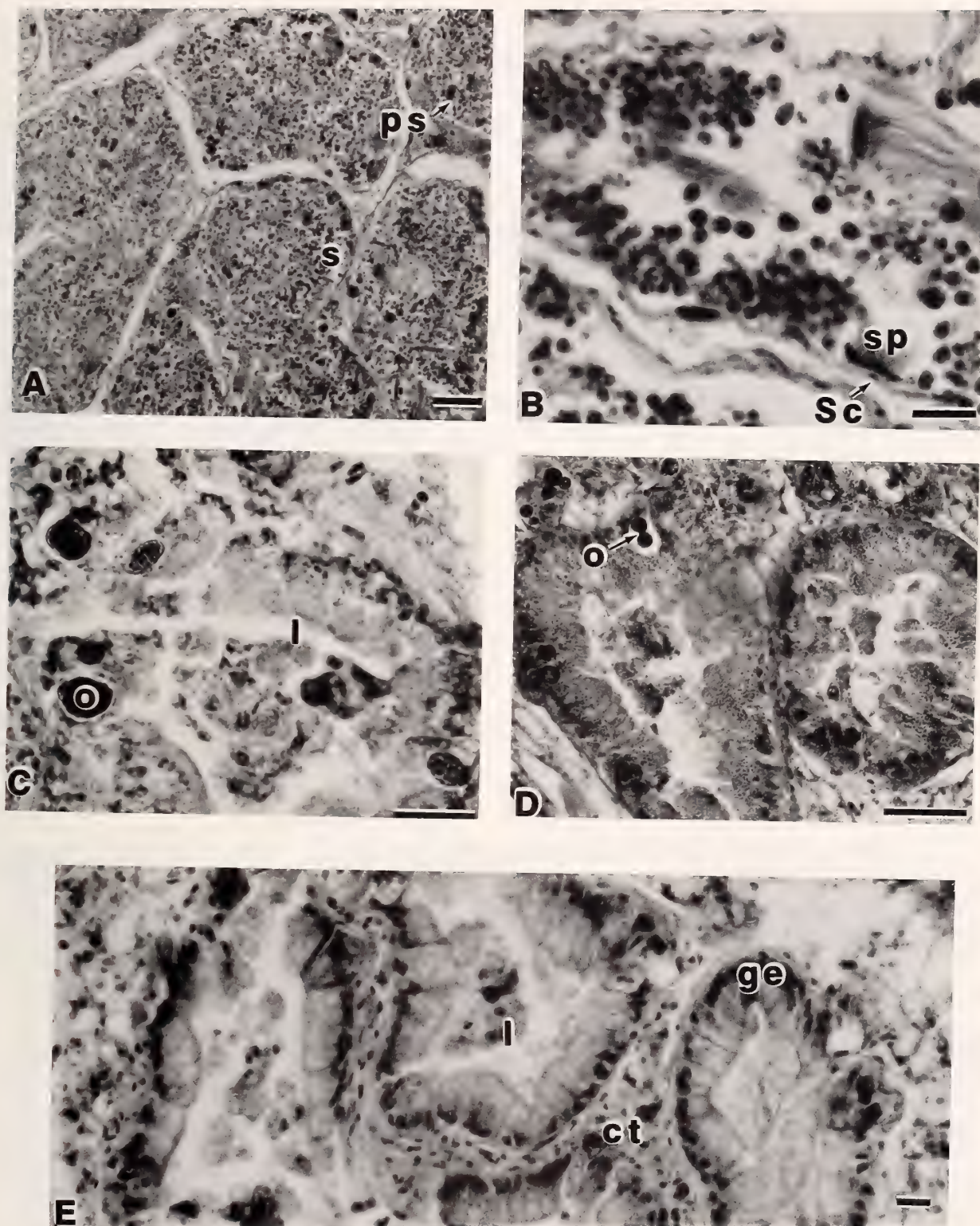
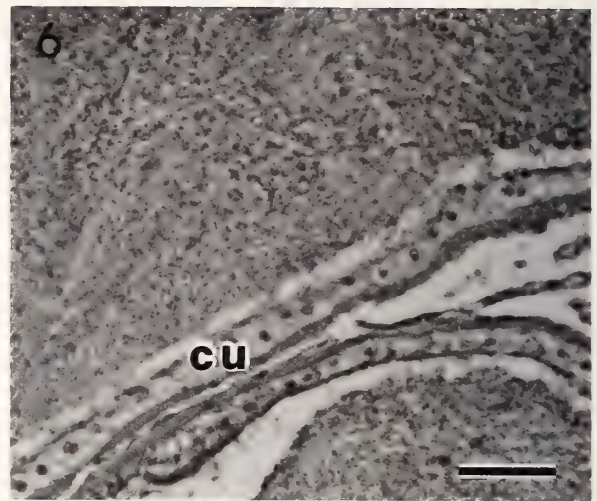


Figure 4

A. Photomicrograph of male acini with spermatogonia and primary spermatocytes, early active stage of the ovotestis (O-1) (scale = 1 mm). B. Acinus with spermatocytes and spermatids attached to the Sertoli cells, late active stage of the ovotestis (O-2) (scale = 0.5 mm). C. Female acinus with mature oocytes, the ripe stage of the ovotestis (O-3) (scale = 0.5 mm). D. Female acini in the release stage of the ovotestis (O-4) (scale = 0.5 mm). E. Irregularly shaped acini of the ovotestis. These acini are not active, atrophy stage (O-5) (scale = 0.1 mm). Key: ct, connective tissue; ge, germinal epithelium; l, lumen; o, oocyte; ps, primary spermatocytes; s, spermatogonia; Sc, Sertoli cells; sp, spermatids.



Explanation of Figures 5 and 6

Figure 5. Photomicrograph of the hermaphroditic duct with the lumen full of spermatozoa. Key: ce, ciliated epithelium; s, spermatozoa (scale = 0.5 mm).

Figure 6. Photomicrograph of the epithelium of the seminal vesicles of the hermaphroditic duct showing the non-ciliated cuboidal cells (cu) (scale = 0.5 mm).

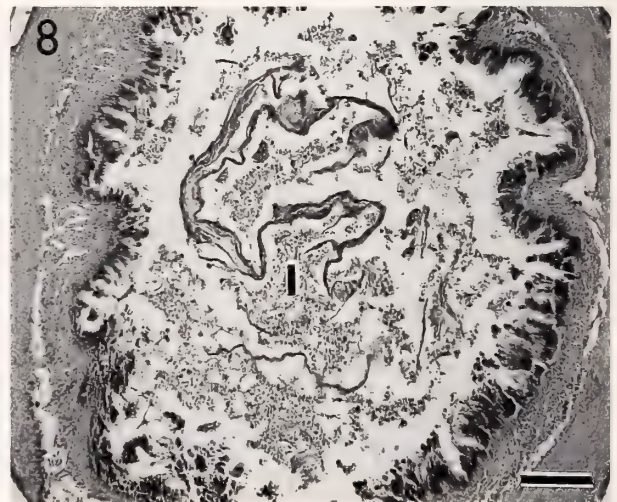
Stages of Activity of the Reproductive Organs

The activity of the reproductive organs of *Caracollus caracolla* can be divided into stages as follows for the ovotestis, spermatheca, and albumen gland.

The ovotestis showed five stages of activity:

(O-1) Early active stage. The walls of the male acini have spermatogonia and primary spermatocytes with large nuclei that stain dark purple with hematoxylin (Figure 4A). The female acini contain oogonia that are very small and stain dark red with hematoxylin.

(O-2) Late active stage. The male acini have secondary



Explanation of Figures 7 and 8

Figure 7. Photomicrograph of the wall and lumen of the spermatheca. Key: L1, layer of cells that border the lumen; L2, longitudinal and circular muscle fibers; L3, layer of cells that border the external wall. Key: l, lumen (scale = 1 mm).

Figure 8. Photomicrograph of a section of the spermatheca showing the degraded material in the lumen (l) (stage S-3) (scale = 0.5 mm).

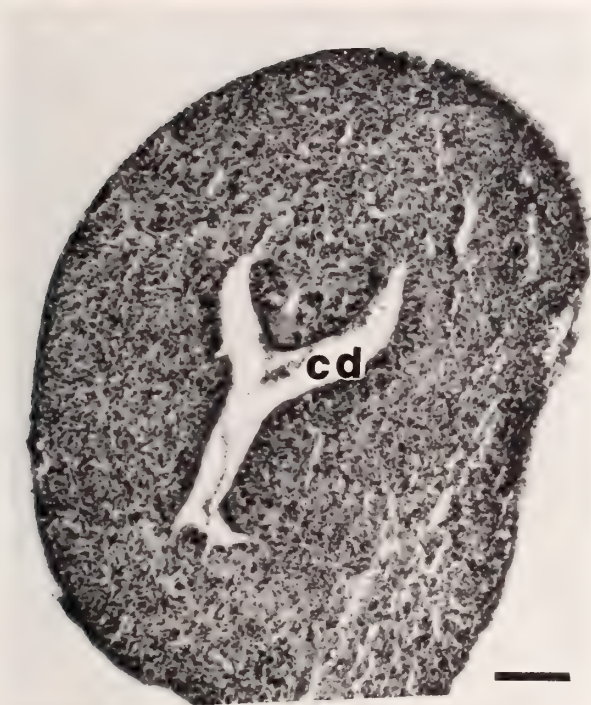


Figure 9

Photomicrograph of a section of the albumen gland in the simple tubular stage (AG-1). Key: cd, central duct (scale = 1 mm).

spermatocytes and spermatids. The spermatids develop in clusters with their heads attached to the Sertoli cells, which are located near the lumen (Figures 3, 4B).

(O-3) Ripe stage. All follicles are expanded and have mature oocytes and spermatozoa in their lumen (Figure 4C).

(O-4) Release stage. Mature gametes are still present in the lumen but they are not as numerous as in the ripe stage (Figure 4D). Some spermatids and vitellogenic oocytes are present near the lumen. The spaces between the acini are filled with mature gametes.

(O-5) Atrophy stage. Most of the acini are empty (Figure 4E).

The spermatheca showed three stages of functional activity:

(S-1) Differentiated stage. The walls are differentiated but the muscle fibers are not completely developed.

(S-2) Mature stage. The organ is large but still empty (Figure 7).

(S-3) Copulation stage. The lumen of the spermatheca is full of residual spermatophore material that comes from the partner at copulation (Figure 8).

The histological study of the albumen gland revealed only two stages of activity:

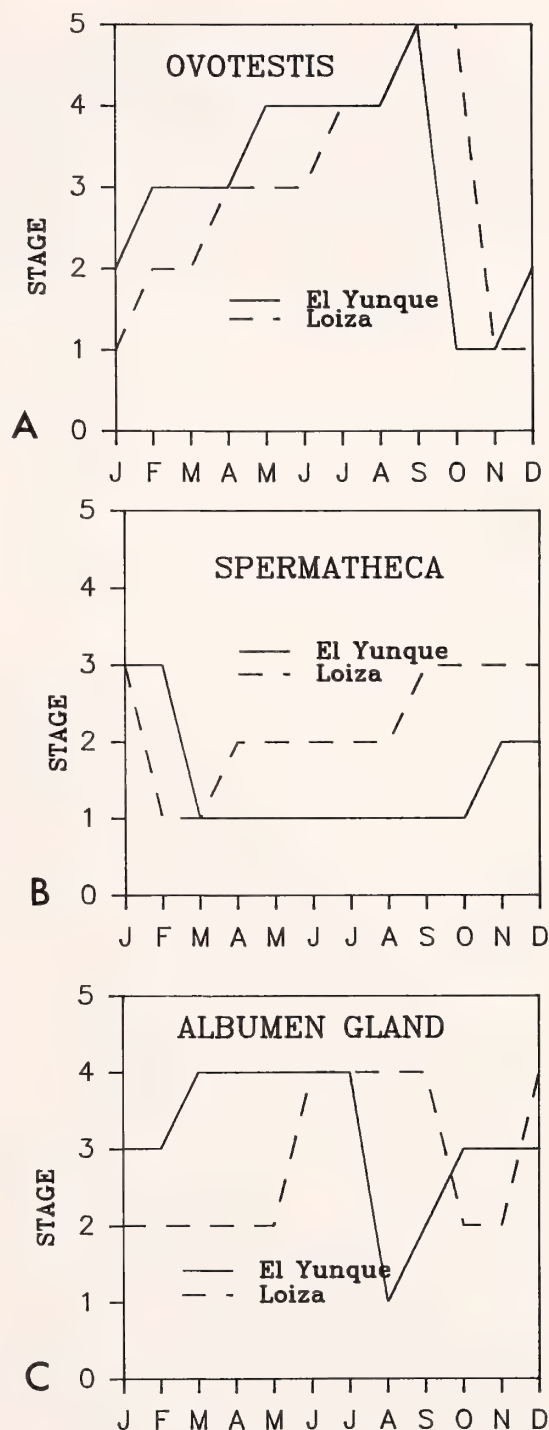


Figure 10

Activity stages of the ovotestis (A), spermatheca (B), and albumen gland (C) for the populations from El Yunque and Loiza. El Yunque = (—), Loiza (---).

Table 1

Two-way analysis of variance testing the effects of different months (climate) and populations (location) on shell and reproductive organ measurements in *Caracolus caracolla*. Key: Ovo, ovotestis; H.d., hermaphroditic duct; Sper, spermatheca; A.g., albumen gland. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.

Source	Month	Population	Month \times population
Shell length	***	*	***
Shell width	***	***	NS
Ovo. length	NS	*	*
Ovo. width	***	NS	*
H.d. length	*	NS	NS
H.d. width	***	*	NS
H.d. weight	NS	*	NS
Sper. length	***	*	***
Sper. width	***	***	**
Sper. weight	***	***	***
A.g. length	***	***	**
A.g. width	***	***	***
A.g. weight	***	***	***

(AG-1) Simple tubular stage. The gland is small with tubules that consist of layers of cells around a central duct (Figure 9).

(AG-2) Compound tubular stage. The cells of the tubules are larger but there is no secretion.

Two additional stages were recognizable with the aid of the gross morphology data:

(AG-3) Secreting stage. The cells start producing secretions; the gland starts swelling.

(AG-4) Mature stage. The cells are full of secretions; the gland is an intense yellow and two or three times larger than at the start of AG-3.

Because the seminal vesicles of the hermaphroditic duct had spermatozoa in the lumen throughout the study period (Figure 5), its activity was not divisible into distinct stages.

The timing of the activity stages was different for the populations from El Yunque and Loiza (Figure 10).

El Yunque population: The early active stage (O-1) of the male acini was observed in the months of October and November (Figure 10A). Most of the acini were in the late active stage (O-2) in December through January. From February to May spermatids appeared in the acini and in the month of June the lumen was filled with spermatozoa (stages O-3 and O-4) and remained filled until August. In September the acini were in the atrophy stage (O-5). The reproductive stages of the female acini were similar to those of the male acini, the only difference being that the oocytes began maturing in May.

The differentiated stage of the spermatheca was observed from March to October (S-1) (Figure 10B). In

November and December the mature stage (S-2) was predominant and in January the lumen was completely filled with residual material (stage S-3).

The albumen gland showed a maximum size and mass in the month of May (stage AG-4) (Figure 10C). In August and September the values of size and mass were minimal (simple [AG-1] and compound [AG-2] tubular stage). The secretory stage (AG-3) probably began in October and lasted until February, when the size and mass of the spermatheca increased. The stages of activity of this gland were reflected in the variation of size and mass throughout the year.

Loiza population: By the beginning of the wet season, November, the male acini appeared to be in the early active stage (O-1) and by February they had spermatids, characterizing the late active stage, (O-2) (Figure 10A). Oo- gonias and spermatogonia were in the ripe stage (O-3) beginning in April. In July, the ovotestes were releasing gametes (stage O-4). Ovotestes in the atrophy stage (O-5) were found in the months of September and October.

The spermatheca were at the differentiated stage (S-1) from February to April, since their lumen was empty and the cells lining the ducts were reduced in size. The mature stage (S-2) was detected because of an increase in the size of this organ, although the lumen was still empty. This stage was observed from April through August. Another characteristic of this stage was that the layer of cells that border the lumen became larger and extended into the lumen. The copulation stage (S-3) was detected because of the presence of material in the lumen; this stage started in September and lasted until January. In this stage the cells that border the lumen were extended and their apices had a material that was continuous with the residual material found in the lumen. It is possible that these cells were absorbing the residual material.

Twice during the year, the albumen gland of snails from the Loiza population had two peaks of activity but no seasonal pattern was evident.

Statistical Analysis of Seasonal Variation

A two-way analysis of variance (ANOVA) revealed the relative effects of seasonal variation in climate ("Month") and location ("Population"), and the interaction of these two (Table 1). The effects were significant for most of the measurements ($P = 0.001$), especially for the spermatheca and albumen gland measurements.

A Principal Component Analysis reduced the number of variables. The variables were divided into two groups: size of the shell (SHELL) and size of the reproductive organs (REPROD). There were two principal components for the SHELL group (SHELL 1 and 2) and three principal components for the REPROD group (REPROD 1, 2, and 3) accounting for a cumulative percentage variance of 96% for SHELL and 70% for REPROD. SHELL 1 varies seasonally, which means that the average shape of

Table 2

Pearson Correlation Coefficients between the principal component of shell measurements (SHELL 1) and principal components of reproductive organs (REPROD 1-4) of *Caracolus caracolla*.

Shell 1 with	<i>r</i>	<i>P</i>
REPROD 1	0.0884	0.2835
REPROD 2	-0.1555	0.0583
REPROD 3	-0.2360	0.0038
REPROD 4	-0.0502	0.5433

the shell of the population is changing throughout the year in both populations. REPROD 1 has positive weighting for the size of the reproductive organs.

To determine if the sizes of the reproductive organs were correlated to shell size, Pearson Correlation Coefficients were obtained between SHELL 1 and REPROD 1-4 (Table 2). The results indicate that the only significant correlation observed was between SHELL 1 and REPROD 3 ($P = 0.0038$). Since REPROD 3 did not show significant effects among the factors that were analyzed, the correlation found between REPROD 3 and SHELL 1 will not be considered. These results suggest that the size of the reproductive organs are not correlated with the size of the shell.

A two-way ANOVA was performed with REPROD 1, 2, and 3 (Table 3). The first principal component of the reproductive organs, REPROD 1, had significant values. The interaction of the population effect in the first component is observed during the months of March to June; July to October the interaction is almost overlapping. From November to February there was no interaction between the populations because they followed a similar pattern of increase and decrease of REPROD 1. There was no significant difference in the effect of month on REPROD 2 ($P = 0.1920$). There was no effect of month ($P = 0.1041$) or interaction between month and population on REPROD 3 ($P = 0.0984$).

DISCUSSION

Histological and gross morphological changes indicate a seasonal variation in most of the reproductive organs of *Caracolus caracolla* from the El Yunque and Loiza populations. Although the pattern of reproductive activity is similar in the two populations, statistical analyses show significant differences in almost all of the measurements of the shells and reproductive organs within each population and between populations. The differences between populations indicate that some external factors probably affect the reproductive activity of these snails.

Environmental Factors

In El Yunque as temperature decreased (October), spermatogenesis and oogenesis began. When the temperature

Table 3

Two-way analysis of variance testing the effects of different months and populations on REPROD 1, 2, and 3 measurements in *Caracolus caracolla*. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Source	SS	DF	MS	<i>F</i> -ratio
REPROD 1				
Month	89.826	11	8.166	3.43**
Population	90.093	1	90.093	37.85***
Month \times population	99.450	11	9.041	3.80***
REPROD 2				
Month	76.136	11	6.921	9.71***
Population	1.227	1	1.227	1.72
Month \times population	42.493	11	3.863	5.42***
REPROD 3				
Month	41.773	11	3.798	4.59***
Population	2.216	1	2.216	2.68
Month \times population	14.810	11	1.346	1.63

began to rise (April), the oocytes were already mature and the spermatids began developing into spermatozoa (Figure 10A). This pattern suggests that an elevation of temperature may be necessary for the maturation of the spermatozoa but that they will not necessarily be mature before the oocytes, as other studies suggest (BOUILLON, 1956; DUNCAN, 1975). In Loiza, although the annual temperature pattern is the same as in El Yunque (Figure 2A), the male and female gametes mature in the same month.

As monthly precipitation increased in El Yunque from 250 mm to 500 mm (April to August), copulation began. In Loiza, the peaks of precipitation were in April and August, which suggest that there might be two seasonal peaks of mating activity.

Maximum activity of the spermatheca was detected in January and February for the population from El Yunque and in September through December for Loiza (Figure 10C). The activity of the spermatheca should be at a maximum when copulation occurs. It is possible that once the sperm are mature (April and May), they are stored in the hermaphroditic duct until August (the month of maximum precipitation). Copulation begins during this month, and by December (in Loiza) and February (in El Yunque) the lumen of the spermatheca is completely filled with degraded material from the spermatophores.

SMITH (1966) described four activity stages for the albumen gland of *Arion ater*. In the present study only the first (AG-1) and second (AG-2) stages could be detected histologically. The secreting (AG-3) and mature (AG-4) stages were determined only by the gross morphology of the gland. The albumen glands of the snails from El Yunque were at the mature stage in March, one month after the spermatheca were at the copulation stage. Since the function of the albumen gland is to secrete the albumen that surrounds the fertilized eggs, it should be active one or

two months after the snails mate (HEATWOLE & HEATWOLE, 1978; TOMPA, 1984). In Loiza, the activity of the albumen gland did not show any seasonal pattern. Although the snails from this dry coastal area showed a seasonal pattern in the activity of the ovotestis and spermatheca, the albumen gland may be active at various times throughout the year so that the fertilized eggs can develop whenever mating occurs.

The high standard deviations show that not all snails had the same state of reproductive activity in each month. It is possible that snails from both populations are mating continually throughout the year, since spermatozoa are always present in the hermaphroditic duct. Nevertheless, according to the activity of the spermatheca, there are some peaks of mating activity in February for the El Yunque population and in December for the Loiza population.

SOLEM & CHRISTENSEN (1984) found that at the beginning of the wet season in Australia there is a marked increase in the size of the ovotestis of camaenids, whereas in this study the size of the ovotestis (length and width) fluctuated throughout the year. In the dry season, especially in March and April, the size of the ovotestis of *Caracolus caracolla* reached a maximum. Just as I observed in the snails of the Loiza population, SOLEM & CHRISTENSEN (1984) found no seasonal change in the size of the albumen gland, probably because both of their sites are arid. The Australian camaenids live in a semi-arid environment that has extensive wet and dry seasons. The dissimilarity in environmental conditions could explain the different reproductive patterns.

HEATWOLE & HEATWOLE (1978) also studied *Caracolus caracolla* in Puerto Rico and determined that the proportion of animals with functional albumen glands is greater in June and July for both populations, but in the present study the population of El Yunque had a greater proportion of functional glands in May. Since the albumen gland is active from March to June, fertilization of the oocytes should have taken place already. Once the sperm are developed in the ovotestis, they are stored in the lobules of the seminal vesicles of the hermaphroditic duct. HEATWOLE & HEATWOLE (1978) observed a greater number of copulations in April (dry season); during the wet season no copulation was observed in the snails from the rain forest. Only three copulations were observed during the wet season in the dry coast population. Their results are in accordance with the results obtained here since there is only one month of difference between copulation and the activity of the albumen gland.

An important characteristic observed in this study and not reported previously is that the male and female sex cells developed simultaneously in separate acini of the ovotestis (Figure 3). Male acini tended to occupy the central position of the ovotestis and the female acini were located in a peripheral position. Previous studies of the ovotestis of pulmonates report that the development of sex cells occurs simultaneously within the same acinus (*e.g.*,

BRIDGEFORD & PELLUET, 1952; LUSIS, 1961; KUGLER, 1965; JOOSE & REITZ, 1969; JONG-BRINK *et al.*, 1976; TOMPA, 1984). Since this is the first histological study of the reproductive cycle of this family, it is not clear whether this feature is unique to *Caracolus caracolla* or represents a characteristic of the family.

The shell and reproductive organs are larger in the snails from El Yunque, but statistical analysis demonstrated no correlation between the size of the shell and the size of the reproductive organs. I expected to find a larger shell in the snails from Loiza since they live in limestone formations (called mogotes) which are an important source of calcium for the construction of shells. This difference in size might be determined by environmental factors that vary between Loiza and El Yunque, such as the type of vegetation, soil characteristics, temperature, or water.

The environmental factor that fluctuated the most throughout the year was precipitation (Figure 2B). Precipitation probably determines the seasonality of reproduction in the camaenids, especially in the Loiza population. This study also reveals a statistically significant difference in the reproductive activity and shell size between the populations of El Yunque and Loiza. The differences could be explained by environmental factors, especially precipitation and relative humidity.

The histological analysis of the four reproductive organs shows that copulation begins earlier in the snails of Loiza (September) than in snails from El Yunque (January). Copulation probably starts earlier in Loiza, ensuring that the eggs are deposited in moist soil before the dry season begins. The snails from El Yunque do not confront this problem since their habitat is moist throughout the year.

These results document changes that occurred during one year. To determine if these changes occur on an annual cycle, however, the study would need to be extended over several years. To determine the effects of the environmental factors on the reproductive cycle of *Caracolus caracolla* controlled studies of temperature, humidity, and day length should be performed.

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The Ecology of Coquina Clams *Donax variabilis* Say, 1822, and *Donax parvula* Philippi, 1849, on the East Coast of Florida

by

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Abstract. Studies on the population ecology of the coquina clams *Donax variabilis* Say, 1822, and *D. parvula* Philippi, 1849, were carried out at a beach transect on the central east coast of Florida. The transect covered the range from the upper intertidal to the offshore subtidal zone, and sampling was done monthly between February 1982 and August 1983. The seasonality in size-frequency distributions (no clear growth pattern, and narrow size ranges) for the two species were similar at all stations. Large individuals (>12 mm) of both species were absent from the offshore stations. The study illustrates the importance of sampling subtidally, as the peak abundances of juveniles and adults of both species were found offshore. Primary juvenile recruitment occurs subtidally, with specimens subsequently migrating into the swash zone as they increase in size. Small individuals (≤ 3 mm), which constituted a substantial portion (46.8%) of *Donax* in all seasons in the present study, should be included in future analyses in order to accurately describe *Donax* populations.

INTRODUCTION

Bivalves of the genus *Donax* (Donacidae) are often an abundant component of the intertidal fauna on sand beaches in many parts of the world (COE, 1953, 1955; WADE, 1967a, b, c; ANSELL *et al.*, 1972; ANSELL & TRUEMAN, 1973; McLUSKY *et al.*, 1975; McLACHLAN *et al.*, 1979). The biology of this genus has recently been reviewed by ANSELL (1983a). Along the east coast of Florida two species are found, namely *Donax variabilis* Say, 1822, and *D. parvula* Philippi, 1849, the separation of which has caused considerable confusion (MORRISON, 1971). ABBOTT (1974) considered *D. parvula* to be merely an ecomorph of *D. variabilis*. The shell morphology of *Donax* species, including *D. variabilis* (CHANLEY, 1969a, b), is known to be quite variable (WADE, 1967c). Comparisons of spatial distributions, morphometrics, and, particularly, allozymes (Nel-

son *et al.*, unpublished data), support the validity of *D. parvula* as a separate species.

Considerably more information is available for *Donax variabilis* than for *D. parvula*. Several studies have examined aspects of burrowing and migratory behavior (PEARSE *et al.*, 1942; TURNER & BELDING, 1957; EDGREN, 1959; TIFFANY, 1971; MIKKELSEN, 1978, 1981, 1985; VEGA & TUNNELL, 1987). Most intertidal populations of *D. variabilis* migrate up and down the beach with the tides, the migratory behavior being stimulated by the acoustic shock of breaking waves. However, two instances of non-migratory populations have been reported (EDGREN, 1959; MIKKELSEN, 1978, 1981). MIKKELSEN (1981) suggests that non-migratory behavior is a local adaptation to deal with a combination of low beach slope and wave energy in areas of irregular semi-diurnal tides and low sand permeability.

Other papers on *Donax variabilis* have examined larval

development (CHANLEY, 1969a), general ecology (EDGREN, 1959), shell polychromism (MIKKELSEN, 1978; SCHNEIDER, 1982), and other shell characteristics (ADAMKEWICZ, 1989). The most detailed study of Florida populations of *D. variabilis* with respect to intertidal distribution, growth rates, and shell color variability is that of MIKKELSEN (1978).

Much of the available information on *Donax parvula* is contained in the taxonomic revision of the genus *Donax*, by MORRISON (1971), but most often this species has not been separated from *D. variabilis*. Some additional information on the abundance, seasonality, and distribution of these two species is available from a number of more recent field studies which have differentiated between *D. variabilis* and *D. parvula* (REILLY & BELLIS, 1978, 1983; SPRING, 1981; LEBER, 1982a, b).

Most studies of *Donax*, including those from Florida (EDGREN, 1959; TIFFANY, 1971; MIKKELSEN, 1978, 1981, 1985), have sampled the intertidal zone exclusively. The present study provides data from a transect including subtidal stations which indicate that a significant portion of the populations for both *Donax* species are located below the intertidal zone. Spatial and seasonal changes in density, together with seasonal size-frequency distributions, are presented and compared for both species.

MATERIALS AND METHODS

Collections of *Donax* were made as a part of a larger benthic sampling study at approximately monthly intervals between February 1982 and August 1983. The sampling location was a moderately exposed sand beach located on the outer coast of the barrier island in Melbourne Beach, Brevard County, Florida. The precise sampling area was located at coastal construction control line survey marker R-140 (28°2'55"N, 80°34'54"W) of the Florida Department of Natural Resources. Water temperature measured in the surf on the dates of sampling varied from 14.5 to 29.5°C, while surf salinity ranged between 34.5 and 35.5‰ (ALLENBAUGH, 1984; PETERS, 1984). Previous biological sampling at this station has been described by SPRING (1981), GORZELANY (1983), and NELSON (1986).

Geological characteristics of the sampling station were extensively studied by STAUBLE *et al.* (1983). Mean tidal range was approximately 1 m, with mean annual wave height being in the range of 0.7 to 0.9 m (STAUBLE *et al.*, 1983). Beach slope on the foreshore ranged between 15 and 25 degrees, depending on the season. Sediment grain size was a coarse sand on the foreshore (mean grain size, 1.8 phi), generally with a region of very coarse shell fragments located in the area of wave break on the shore. Offshore, sediments were a fine sand (mean grain size, 3 phi) (STAUBLE *et al.*, 1983). Organic content of the sediment was approximately 0.5% (Nelson, unpublished data).

At the study area, a transect line was established perpendicular to the shore, and four replicate 20.3-cm-diameter cores were taken at the high-tide line, at the base

of the region of wave run-up on the beach (swash zone, approximately 30 m below the high-tide line), and at distances of 61 m (200 ft) and 91 m (300 ft) from the high-tide line. Water depths at the 61 and 91 m sites were in the range of 1.5–3 m. All samples were taken during low tide, and sieved in the field through a 0.5-mm-mesh screen, fixed in 10% formalin, re-sieved through a 0.5-mm-mesh screen in the laboratory, and stored in a 70% ethanol-rose bengal stain solution until sorted.

Small individuals (<3 mm) could not always be assigned to one species, and most small specimens were classed as ("small") *Donax* spp. Shell length was measured with an optical micrometer. Dry weight was measured after drying the specimens at 100°C for 24 hr. After weighing, the samples were combusted at 500°C for 3 hr before measuring the ash-free dry weight. Weight determinations were done for *Donax variabilis* only, as the material for *D. parvula* contained too few individuals to cover the entire range of the total size-frequency distribution of the population.

Simple linear regression equations relating log-transformed shell length and weight (wet-, dry-, and ash-free dry weight) for *D. variabilis* were computed (SOKAL & ROHLF, 1981).

RESULTS

Abundance Patterns

The seasonal patterns of abundance for *Donax variabilis*, *D. parvula*, and *Donax* spp. (unidentifiable juveniles of *D. variabilis* and *D. parvula*) are presented in Figures 1–3. Individuals of both species were only rarely collected from the high-tide line (possibly due to a downshore migration during low tide), and data from this station are not presented.

For *Donax variabilis* in the swash zone, a peak density was observed in February 1982, with relatively lower densities being found for the rest of the sampling period. The patterns of abundance at the 61-m and 91-m locations were broadly similar. The highest abundances were found in the April–May period, both in 1982 and 1983. At the 91-m station, there was also a peak in abundance in December 1982. On most sampling dates, densities were greater at the offshore stations than at the swash-zone station (maximum density of 3550 individuals/m² at the 61-m station in May 1983).

The pattern for *Donax parvula* was less consistent among stations. Peaks of density occurred in February and October 1982 in the swash zone. At the 61-m location, the maximum density occurred in November 1982, with secondary peaks in August 1982 and 1983. At the 91-m station, abundance was greatest in August 1982 and 1983. The maximum density observed for *D. parvula*, from the swash zone (February 1982), was 1416 individuals/m².

Donax spp. (<3 mm) were never found at the high-tide station and were only rarely found in the swash zone. At

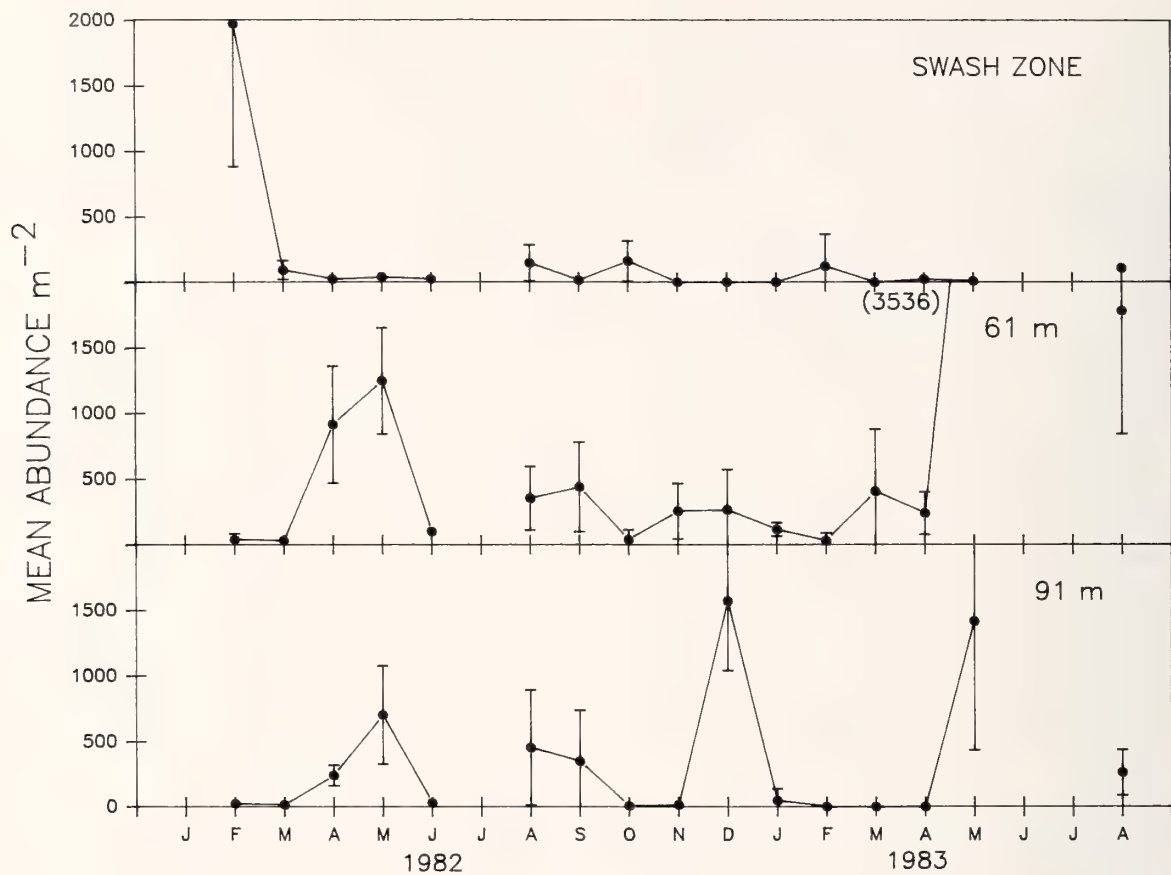


Figure 1

Spatial distribution of *Donax variabilis* between February 1982 and August 1983 along the sampled transect (swash zone, 61 m, 91 m).

the 61-m station, the greatest abundances were found from May through September. Density at 91 m was variable, with maxima being found in April, September, and November 1982, while abundance in 1983 was uniformly low. The maximum density (59,136 individuals/m²) was observed at 61 m during August 1982.

Donax variabilis tended to be somewhat more abundant than *D. parvula* on most sampling dates. Small *Donax* spp. were generally more abundant than larger specimens of either species, and constituted 46.8% of the total individual count. The small individuals, although pooled for both species (as no distinction in recruitment to the two species can be made), are an important proportion of these populations and one that has been widely neglected in previous studies on *Donax*.

Size-Frequency Distributions

Within the three categories (*Donax variabilis*, *D. parvula*, and *Donax* spp.), size-frequency distributions for the swash zone, 61-m, and 91-m stations were similar in almost all cases. Therefore, data from all three locations were pooled

for the size-frequency histograms presented in Figure 4. The only exception involved *Donax variabilis*, for which a total of 15 specimens of >12 mm length were found in the swash zone during the entire sampling period from February 1982 through August 1983. Because these specimens represented only 0.9% of the total number of *D. variabilis*, and because no specimens of *D. parvula* of >12 mm length were found (13.5–22.5 mm), these 15 individuals are not displayed in Figure 4 in order to standardize the graph axes.

The patterns of size-frequency distributions for *Donax variabilis* were generally similar between 1982 and 1983. In 1982, the mean size decreased in April and shifted to a still smaller size class in August, reflecting the heavy recruitment taking place at this time (Figure 4, August 1982). The size distributions were generally similar from September through December, while January and February 1983 showed a slight shift in the mean to a larger size. Unlike in 1982, when the shift occurred in April, a shift to smaller size classes occurred in March 1983. The mean size remained low through May, and shifted to an even smaller size category in August 1983.

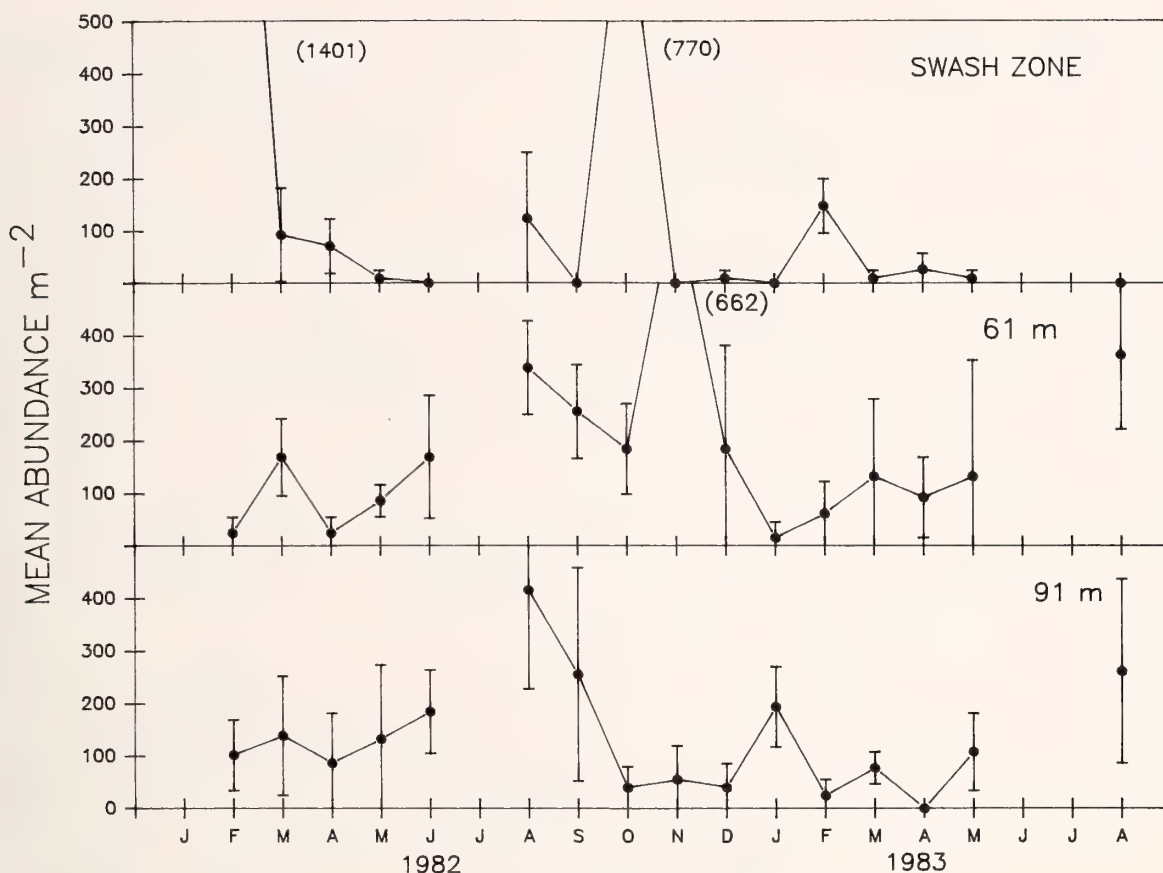


Figure 2

Spatial distribution of *Donax parvula* between February 1982 and August 1983 along the sampled transect (swash zone, 61 m, 91 m).

For *Donax parvula* the annual patterns of changes in the size-frequency distributions were generally similar in both the years sampled (Figure 4). The mean of the size-frequency distribution tended to increase from the late fall (e.g., November 1982) until March, when it reached the annual maximum. From March through the summer, and even until October, the mean size tended to decrease.

For the small *Donax* spp. (Figure 4), there was a slight increase in the mean size from February through May 1982, with a decrease to smaller mean size during June through August. The mean size was somewhat higher from September through December. In January 1983, the size-frequency distribution of the juveniles was strongly skewed to the smallest size class, suggesting the occurrence of recruitment (Figure 4). By March, the mean had increased again. During spring and summer 1983 (April–August), mean size was in the size interval of 1.5 mm, as it had been in the period June–September 1982. The shifts to smaller mean sizes suggest recruitment of new individuals to the population. The strong peak of juveniles in the 1.5-mm size class, together with the extremely high density recorded in August 1982 (about 60,000/m²), suggests that

heavy settlement had occurred in July (Figure 4). Thus the size-frequency distributions of the juveniles clearly indicate principal periods of recruitment, but also show a constant input of recruits to the subtidal populations of *D. variabilis* and *D. parvula*.

Length–Weight Relationships and Growth Rates for *Donax variabilis*

The regressions for size (maximum shell length) and weight (wet weight; $y = 0.107x^{3.195}$, $r = 0.99$, dry weight; $y = 0.08x^{1.90}$, $r = 0.99$, and ashfree dry weight; $y = 0.041x^{2.382}$, $r = 0.99$) all show highly significant positive correlations, illustrating a population of individuals with active tissue growth throughout the size range collected. This relationship is in good accordance with the general biology of other species of *Donax*. ANSELL (1983b) showed that many species of *Donax* have species-specific growth curves. Growth rates of 3.7 mm/month have been reported for *D. variabilis* from Florida (MIKKELSEN, 1978, 1985). The size distributions and mean sizes per month, however, do not allow for an accurate growth analysis, owing to the

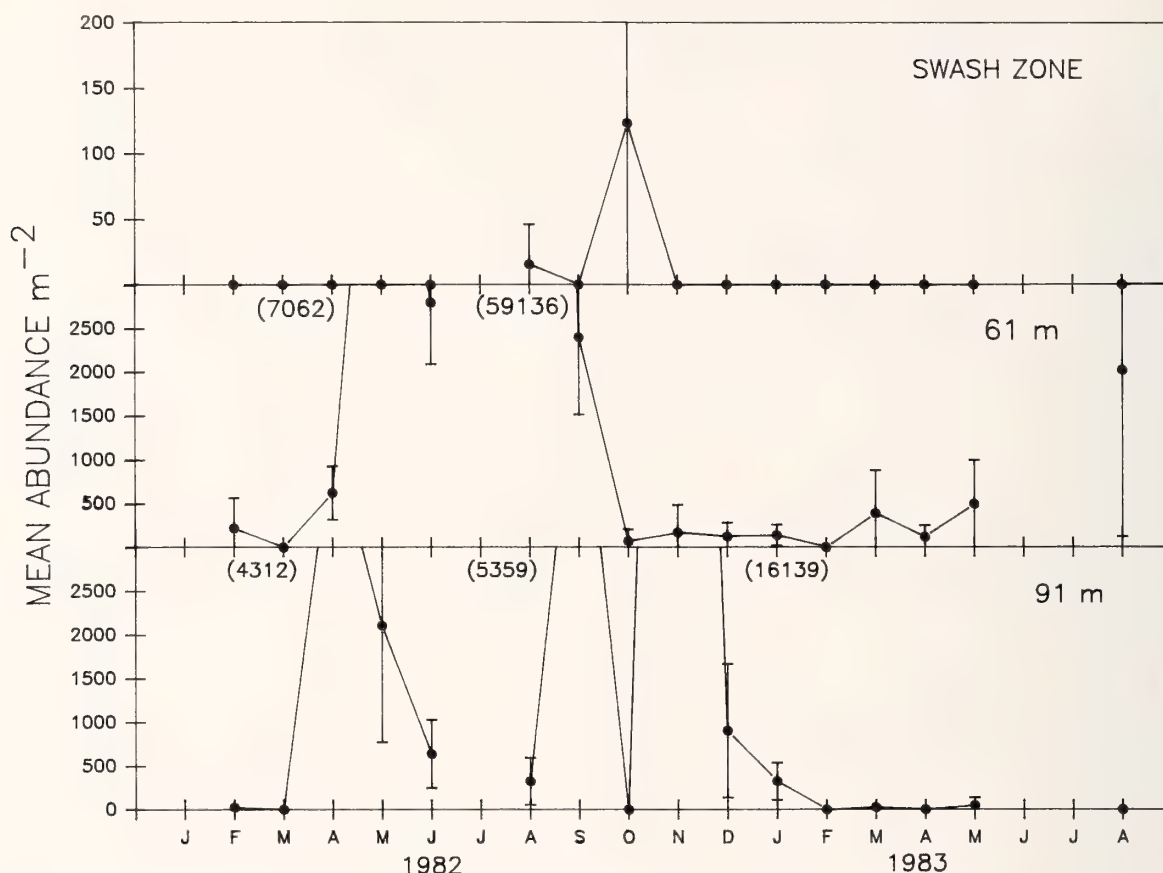


Figure 3

Spatial distribution of small *Donax* spp. between February 1982 and August 1983 along the sampled transect (swash zone, 61 m, 91 m).

constant input of small individuals into the population. On the basis of the mean sizes of the individuals, the maximum change in mean size in the present study was 3.43 mm.

DISCUSSION

Distribution and Abundance

Donax variabilis is distributed from the coast of Virginia to the coast of Mississippi (MORRISON, 1971). CHANLEY (1969b) suggested that this species may exhibit summer range extensions as far north as Long Island, and JACOBSEN (1955) described such a population, calling it *Donax fossor*. MORRISON (1971) suggested that *D. variabilis* has a two-year life-span, and that in some cases individuals may survive a third year, whereas ANSELL (1983a) reported a one- to two-year life cycle. MIKKELSEN (1978, 1985) estimated that *D. variabilis* in Florida grow at a rate of 3–3.7 mm/month in the summer months. The present data, with high numbers of recruits and small mean sizes throughout the year, support the previous reports on rapid

growth rates and a short life-span, because no senescence was recorded among the individuals. MIKKELSEN (1978) suggested that this species spawns in February with a three-week larval period, resulting in a March settlement. He also suggested that Florida *D. variabilis* has a second spawning in June. LEBER (1982a) recorded juvenile recruitment to a North Carolina population as occurring in February and November. The February settlement was indicative of a winter spawn. He suggested that two-year-old individuals move into the intertidal swash zone in March after overwintering in the shallow offshore zone. MATTA (1977) observed a June settlement of spat of *D. variabilis* in Duck, North Carolina.

Donax parvula is recorded from Ocracoke, North Carolina, to St. Lucie County, Florida, and is reported to have a two-year life-span (MORRISON, 1971) possibly spawning somewhat later than *D. variabilis*. However, LEBER (1982a, b) indicated that recruitment in a North Carolina population occurs in February, as it did for *D. variabilis*, although the two species have different abundance maxima (*D. parvula* in May–July, and *D. variabilis* in August–

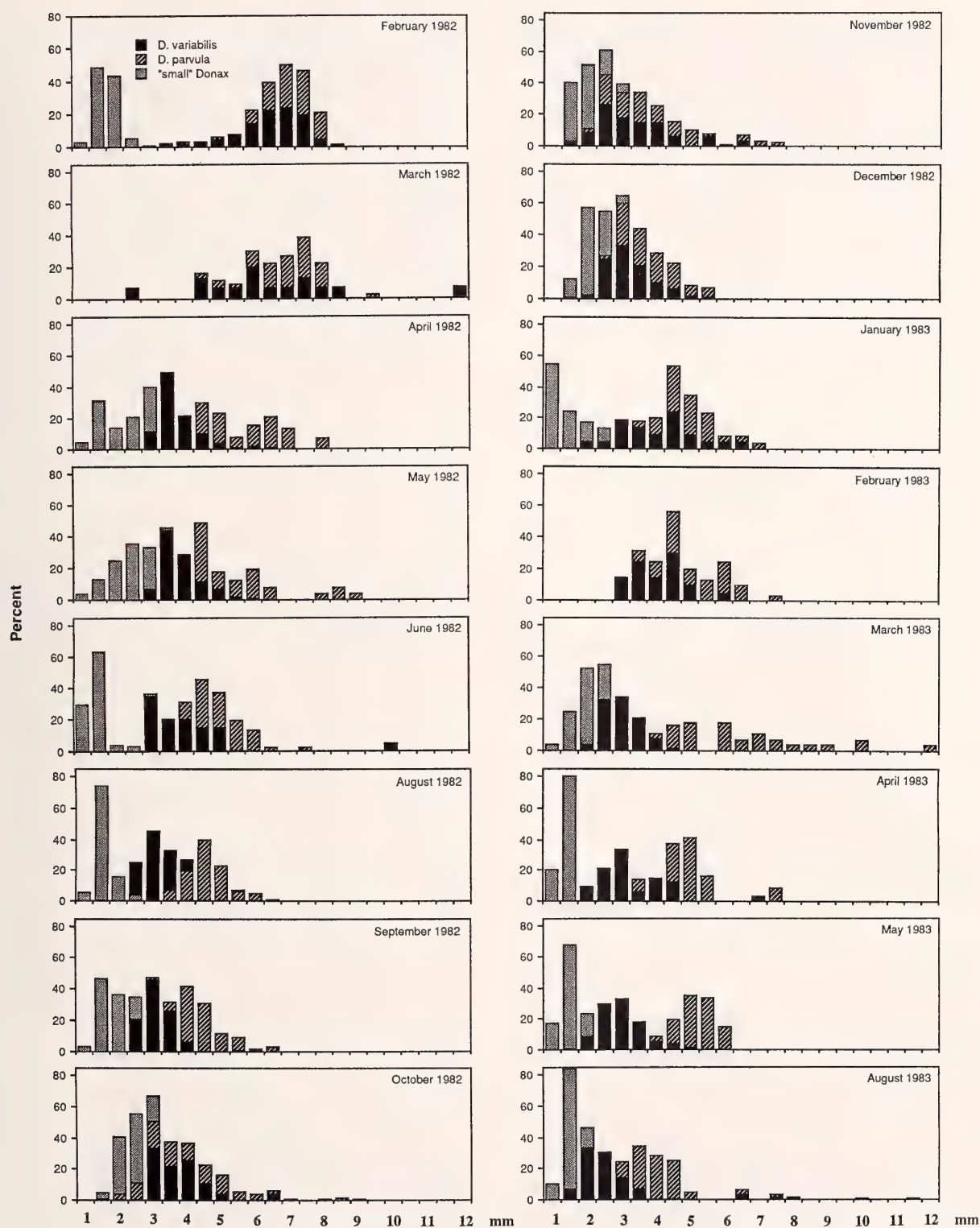


Figure 4

Size-frequency (percent) distribution (0.5-mm classes) of *Donax variabilis* (black bars), *D. parvula* (striped bars), and small *Donax* spp. (shaded bars) from all sampled dates (data pooled for all stations along the transect studied). The percent values are relative as to the actual numbers of each category to allow for direct comparisons.

September). REILLY & BELLIS (1978, 1983) also observed young of both *Donax* species recruiting during March in North Carolina.

A review of available seasonal abundance data from a variety of locations (NELSON, 1985) indicated that both *Donax variabilis* and *D. parvula* tend to achieve maximum densities during the summer (June–July) in most locations. The present study suggests an earlier period (April–May) for peak abundances of *D. variabilis* at Melbourne Beach, Florida. *Donax parvula* generally showed later maxima, in the period from August through November and again in February. The broad period of abundances for small individuals (April–November) suggests an extended period of recruitment, given MIKKELSEN's (1978, 1981, 1985) estimates of growth rates. The differences observed here as compared with other studies may be in part due to different temperature regimes at different locations and/or differences in food availability for the clams. Also important is that subtidal areas were included in this study, whereas they were not in the other studies.

Recorded maximum densities for *Donax variabilis* range from 166 to 13,114 individuals/m² (NELSON, 1985), whereas estimates of density for *D. parvula* range from 401 to 1425/m². Density estimates from the present study fall within the maximum ranges for both species (MIKKELSEN, 1978, 1981) and the total abundance of *Donax* spp. during the sampling period in 1982–1983 did not differ from previous records from the same area (GORZELANY, 1983; NELSON, 1986), although the relative proportions between the species has varied over time. Generally the published records of population densities of the species do not include recruits, however, and in the present study such recruits made up a substantial portion of the population throughout the investigated period (average 46.8%), adding almost 60,000 individuals/m² at the peak value. Wide ranges of density values for *D. denticulatus* at different locations have been shown to depend partially on environmental factors, such as particulate organic carbon (SASTRE, 1984).

Size-Frequency Distributions

The seasonal patterns of the size-frequency distributions for *Donax parvula* and *D. variabilis* were very similar (Figure 4). Neither species showed clear evidence of an increase in average size except for the late winter–early spring period. For both species, the mean size tended to decrease after March until the following fall. This size shift corresponds to the period when the largest numbers of small *Donax* spp. were found. The presence of very small clams in the subtidal population virtually year round suggests that although the major period of recruitment may occur in the summer, recruitment to the populations may take place throughout the year. This agrees with ANSELL's (1983a) observation that the typical spawning pattern for *Donax* consists of repeated incomplete spawnings by individuals over an extended spawning season, in contrast

to the statement by SASTRE (1984) that *D. denticulatus* from Puerto Rico would be the only known species of *Donax* with continuous recruitment.

Two factors may contribute to the absence of large individuals (>12 mm) from the subtidal populations (stations at 61 m and 91 m offshore). Predation by bottom-feeding fish, which commonly have *Donax* in their guts (NELSON, 1986), may fall heaviest on the larger size classes. Alternatively, clams may migrate shoreward as they reach larger sizes. LEBER (1982a) suggested an opposite migration pattern with an offshore migration of *D. parvula* in winter. The size-frequency distributions for *D. variabilis* collected from the swash zone at a nearby beach by MIKKELSEN (1978) suggest that migration may be important. Mikkelsen's samples (April–September only) indicated that the bulk of the population of the intertidal zone was larger than 12 mm. Since initial recruitment of *Donax* appears to occur largely subtidally in this area, large intertidal individuals are most likely the result of migration from offshore, with subsequent growth in the swash zone, thus avoiding predation by fish.

ACKNOWLEDGMENTS

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“*Solen rosaceus*”—Three Species

by

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Abstract. The small jackknife clams living on the coast of southern California, the outer coast of Baja California, and in the Gulf of California, and known as “*Solen rosaceus* Carpenter, 1864,” belong to three different species: the allopatric species pair *S. (Ensisolen) rosaceus* Carpenter, 1864, from southern California, and *S. (E.) gemmelli* sp. nov. from the upper Gulf of California (San Felipe area), and the variable and widespread *S. (E.) rostriformis* Dunker, 1862, from southern California to La Paz. The subgenus *Ensisolen* Habe, 1977, is redefined. Neotypes of *Solen rosaceus* Carpenter, 1864, and *Solen lappeanus* Dunker, 1871, are designated.

INTRODUCTION

During preparative work for a revision of the western American Solenidae, I examined over 150 specimens of the small jackknife clams commonly arranged in collections and published in identification books and faunal lists under the name “*Solen rosaceus* Carpenter, 1864.” In spite of many citations, illustrations of these small bivalves are rather scarce. For example, the clam was not figured in such classic works as KEEP (1887, 1904), GRANT & GALE (1931), OLDROYD (1925), KEEP & BAILY (1935), and ABBOTT (1954), and also not in some of the smaller and more general field guides, such as ABBOTT (1968); the figures in KEEN (1958, 1971), MCLEAN (1969), and POHLO (1963) are not accurate.

There are, in fact, three species involved, which are quite close but differ in several constant characters. One species is described as new; the other two are redescribed and their taxonomy discussed. All belong to the subgenus *Ensisolen* Habe, 1977, which is redefined herein.

Abbreviations used in the text: AMNH—The American Museum of Natural History, New York; BMNH—British Museum (Natural History) (now “The Natural History Museum”), London, Great Britain; CAS—California Academy of Sciences, San Francisco; LACM—Los Angeles County Museum of Natural History, Los Angeles; MCZ—Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts; MNHN—Muséum National d'Histoire Naturelle, Paris, France; SDNHM—San Diego Natural History Museum, San Diego; UCB—University of California, Berkeley; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZIM—Zoologisches Institut

und Museum der Universität Hamburg, Hamburg, Germany; ZMB—Zoologisches Museum der Humboldt-Universität Berlin, Berlin, Germany.

TAXONOMY

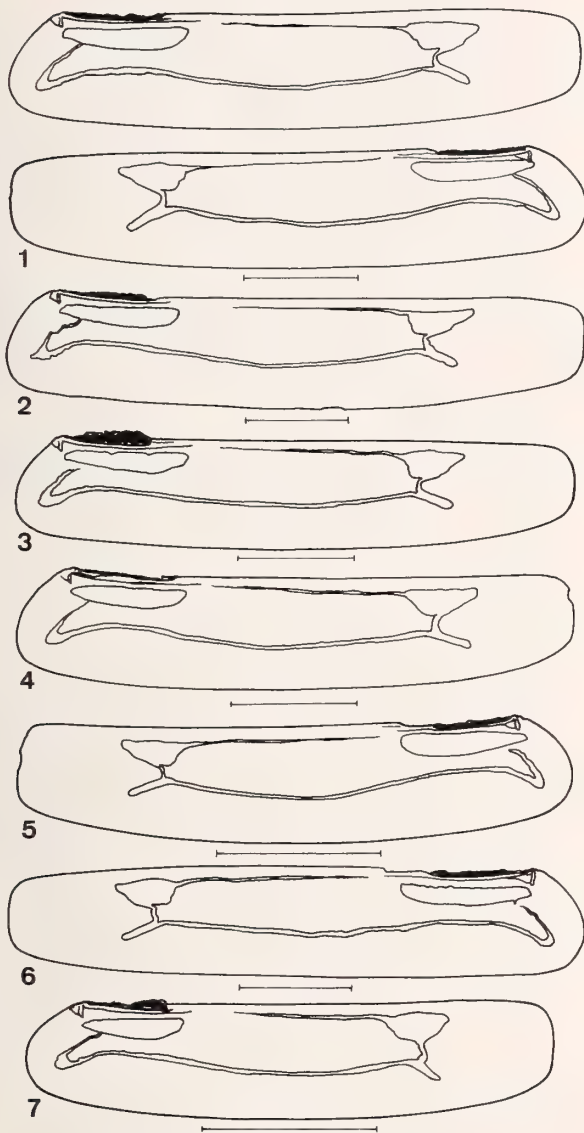
Genus *Solen* Linné, 1758

Solen LINNÉ, 1758:672.

Type species: *Solen vagina* Linné, 1758, by subsequent designation, Schumacher, 1817, central Indo-Pacific (see Figure 62 herein).

Approximately 65 Recent species, worldwide, mostly tropical and warm-temperate.

Shells small to very large, thin and fragile to solid, in shape variable but in general outline somewhat rectangular, from extremely long and narrow to rather short. Dorsal and ventral margin straight and parallel, straight and very slightly tapering, or valves more or less curved with convex ventral margin and dorsal margin concave, straight, or convex. Shells gaping at both ends. Anterior and posterior margin truncated or rounded to semicircular; truncated margins vertical or positively or negatively oblique. Beaks terminal, in species with semicircular anterior margin appearing slightly subterminal. Hinge and ligamental area straight or slightly bent dorsally. Exterior with or without a more or less pronounced furrow parallel to the anterior margin or with a slight depression only. Anterior adductor scar long-oval to very long and slender. Posterior adductor scar oval to triangular, situated above the posterior pallial line and united with the dorsal limb of the pallial sinus or situated in front of the posterior pallial line and separated from the pallial sinus. Pallial



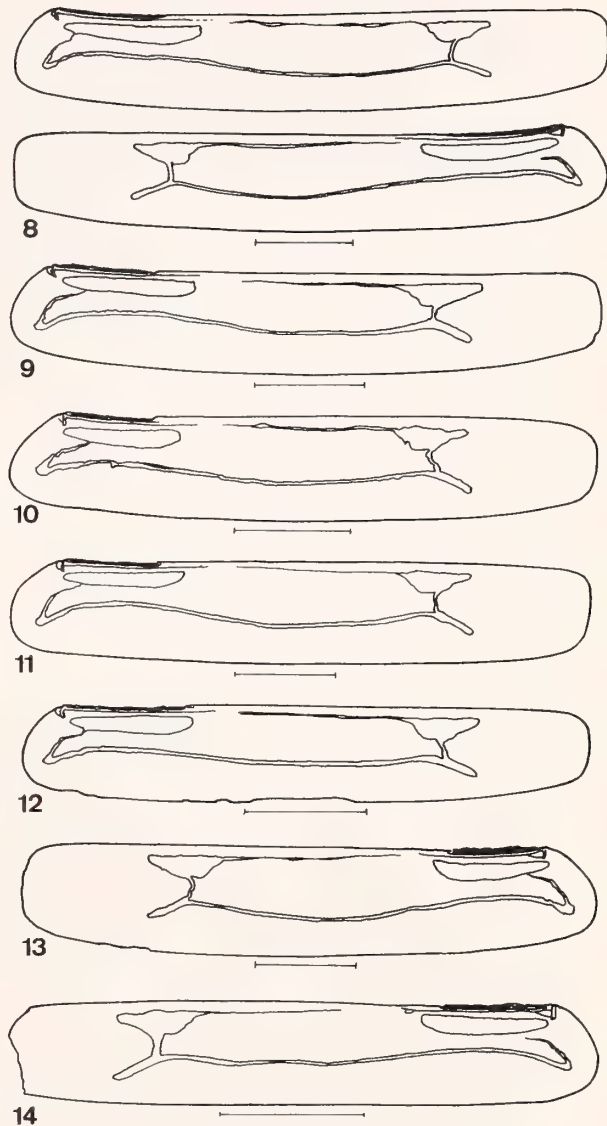
Explanation of Figures 1 to 7

Figures 1–7. *Solen rosaceus* Carpenter, all from California. Scale = 10 mm. Figure 1. San Pedro, Los Angeles (no data), neotype MNHN. Figure 2. San Diego (no data), AMNH 26307 (figured specimen in EMERSON, 1981:pl. 121, fig. 9). Figure 3. San Pedro, leg. E. P. Chace, MCZ 51594. Figure 4. San Pedro, leg. H. N. Lowe, 13 December 1924, MNHN, ex Staadt coll. Figure 5. San Diego, AMNH 26317, ex Oldroyd coll. Figure 6. San Pedro (no data), MNHN. Figure 7. Anaheim Landing, leg. E. P. Chace, MCZ 67379.

sinus short to very short, triangular, trapezoid or nearly square. Hinge with one cardinal in each valve, no laterals. Periostracum thin, in fully grown specimens of larger species rather thick and strong.

Subgenus *Ensisolen* Habe, 1977

Ensisolen HABE, 1977:228 [in Japanese].



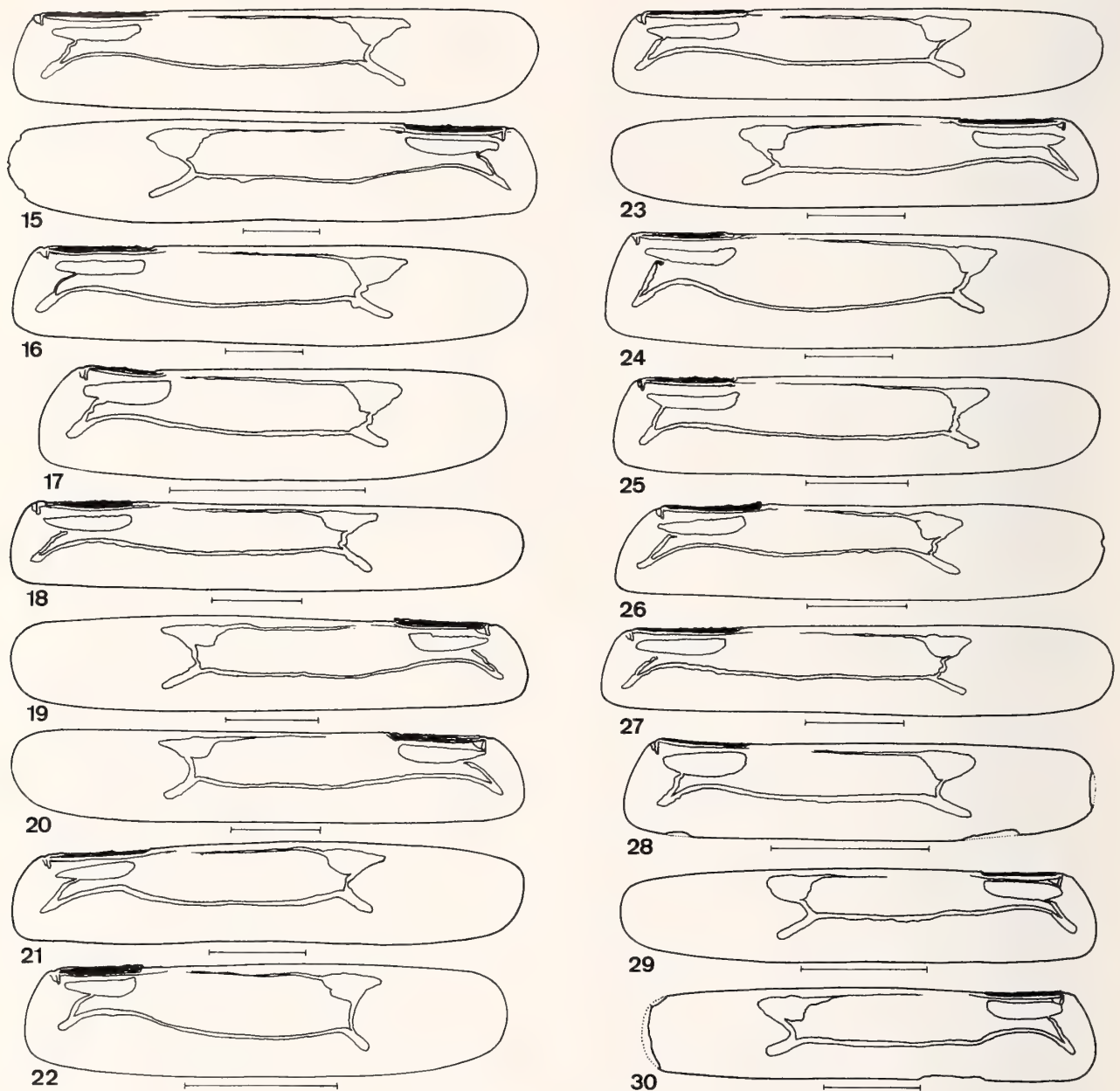
Explanation of Figures 8 to 14

Figures 8–14. *Solen gemmelli* Cosel, sp. nov., all from the San Felipe area, Baja California, Mexico. Scale = 10 mm. Figure 8. San Felipe, between Playa Alicia and El Paraiso, on sand bars at low tide, leg. Gemmell, holotype SDNHM. Figures 9–13. Same locality as in Figure 8, paratypes SDNHM. Figure 14. 32 km S of San Felipe, intertidally, leg. F. B. Howard, April 1957, LACM 104778, ex Kanakoff coll.

Type species: *Solen krusensterni* Schrenck, 1867, by original designation. Northern Japan, northward to Siberia, Ochotsk Sea (see Figure 60 herein).

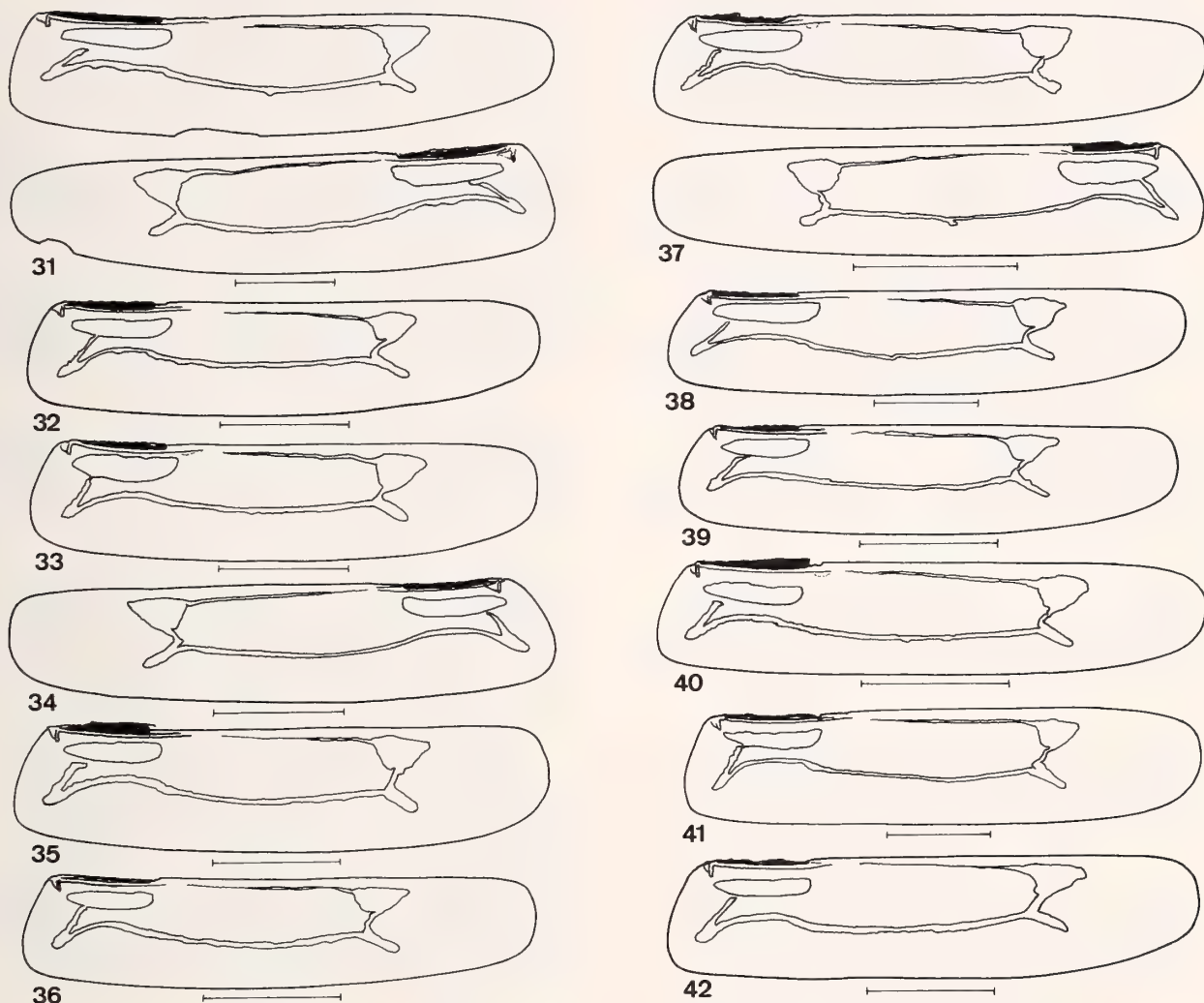
Fourteen to sixteen species, northwestern Pacific, eastern Pacific, western Atlantic.

Shells small to medium-sized, elongate to very elongate, and variable in length–width ratio, straight to somewhat curved, with general aspect like a short *Ensis*. Anterior margin rounded-truncate to nearly semicircular, posterior



Explanation of Figures 15 to 30

Figures 15-30. *Solen rostriformis* Dunker, "San Diego," "San Felipe," and "Mazatlan" forms. Scale = 10 mm. Figure 15. Santo Domingo, outer coast of Baja California, Mexico, *leg.* C. R. Orcutt, SDNHM 15442. Neotype of *Solen lappeanus* Dunker, 1871. Figure 16. Same locality as in Figure 15, SDNHM 15442. Figure 17. Bahia Concepcion, 1.6 km S of Punta Santo Domingo, AMNH 78609. Juvenile with shorter and broader shell. Figure 18. Upper Newport Bay, Orange Co., California, LACM 104777. Figure 19. Santa Barbara, California, *leg.* Forrer, ZMB, *ex* Dunker coll. Figure 20. Morro Bay, California, *leg.* M. & E. Caruthers, 1937, ZIM. Figure 21. San Diego Bay, California, MCZ 140200. Figure 22. San Diego Bay, California, 16-20 m, *leg.* C. A. Kofoid & W. J. Raymond, 13 July 1901, CAS IZ039968. Figure 23. 32 km S of San Felipe, Baja California, Mexico, *leg.* F. B. Howard, April 1957, LACM 104778. Figure 24. San Felipe, Baja California, *leg.* H. N. Lowe, 1933, SDNHM 22576. Figure 25. San Felipe Bay, Baja California, between Playa Alicia and Pete's Camp, sandbars at edge of low tide, *leg.* Gemmell, 1964-1975, SDNHM 90140. Figure 26. 40 km S of San Felipe, Baja California, *leg.* E. P. Chace, March 1957, MCZ 215041. Figure 27. Same locality as in Figure 23. Figures 28-30. Mazatlan, Sinaloa, Mexico, on beach, *leg.* L. G. Hertlein, 8 December 1932, CAS IZ039969.



Explanation of Figures 31 to 42

Figures 31-42. *Solen rostriformis* Dunker, southern "La Paz" form. Scale = 10 mm. Figure 31. Holotype BMNH 19771, no locality. Figures 32-35. La Paz, Baja California, Mexico, SDNHM 71460. Figure 36. El Magote, Puerto de La Paz, Baja California, Mexico, 24°10'N, 112°W, intertidal to 2.5 m, leg. McLean *et al.*, 11 April 1966, LACM 66-29. Figures 37, 38. Bahia Magdalena, Baja California Sur (outer coast), intertidal sand flat, 0.8 km S of pier at Puerto San Carlos (24°47.4'N, 112°6.3'W), leg. C. Swift, 3 November 1971, LACM 71-186. Figure 39. Estero de Punta Banda, outer coast of Baja California (31°46.6'N, 116°37.3'W), leg. McLean, 20 December 1964, LACM 64-33. Figures 40, 41. Bahia Cholla, Puerto Penasco, Sonora, Mexico, AMNH 178035. Figure 42. Bahia Cholla, leg. R. B. Beck, MNHN, ex Staadt coll.

margin truncate, with rounded corners to well rounded or nearly semicircular. Dorsal margin somewhat concave to slightly convex, ventral margin always slightly to markedly convex. Posterior third or fourth of the valve more or less tapering. Hinge and ligamental area slightly bent dorsally. No sharp furrow parallel to the anterior margin, but sometimes with a very shallow, more or less broad depression. Posterior adductor scar always above the pallial sinus and united with its dorsal limb.

The short diagnosis by HABE (1977) gives as the distinguishing feature for *Ensisolen* only the anterior of the

shell, which is slightly curved and prolonged towards the anterior; in contrast, *Solen* has a truncate anterior. Further differences between *Ensisolen* and all other *Solen* (at this time maintained under this genus without other subgenera, although a subdivision would be necessary) are the situation of the posterior adductor scar above the pallial sinus and not in front of it, the more or less ensiform outline, and the lack of a deep and pronounced furrow along and parallel to the anterior margin. The anterior margin is indeed never straight and sharply truncate as in several other *Solen* (see Figures 62 and 63; for more examples,



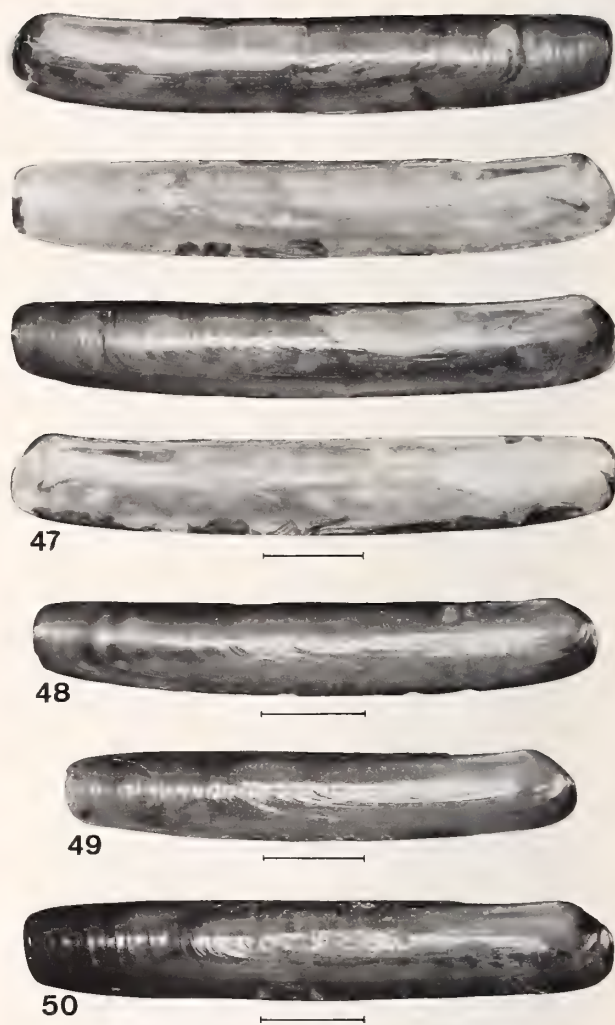
Explanation of Figures 43 to 46

Figures 43-46. *Solen rosaceus* Carpenter. Scale = 10 mm. Figure 43. Neotype MNHN, San Pedro, California, *leg.* H. N. Lowe, 23 December 1924 (*ex* Staadt coll.). Interior and exterior of both valves. Figures 44, 45. Terminal Island, Los Angeles, California, *leg.* W. H. Eshnaur, 28 July 1928, MNHN, *ex* Staadt coll. Exterior of two left valves. Figure 46. San Diego, California, AMNH 26317, *ex* Oldroyd coll. Exterior of a left valve.

see COSEL, 1989:195, 196, 198) but at least somewhat convex. In *Ensisolen*, the anterior and posterior corners are always more or less rounded (which makes, together with the often curved shell, the "ensiform" outline). The dorsal and ventral margins are never strictly parallel from end to end: the posterior taper is always more or less marked.

Solen (Ensisolen) rosaceus Carpenter, 1864

S. sicarius var. *rosaceus* CARPENTER, 1864:536, 638 (reprinted 1872:22, 124); CARPENTER, 1865:177 (reprinted 1872:279).



Explanation of Figures 47 to 50

Figures 47-50. *Solen gemmelli* sp. nov., all from the San Felipe area, Baja California, Mexico. Scale = 10 mm. Figure 47. Holotype, SDNHM 90139. San Felipe, between Playa Alicia and El Paraiso, on sandbars at low tide, *leg.* Gemmell. Interior and exterior of both valves. Figures 48-50. Three paratypes, SDNHM 90139, same locality. External views of right valves.

S. rosaceus: MORRIS, 1952 (1960):55, pl. 15, fig. 4; MORRIS, 1966:39, pl. 23, fig. 2; ABBOTT, 1974:495, no. 5634 (fig.); EMERSON, 1981:681, pl. 121, fig. 9.

Type material: The material on which Carpenter's description is based is indicated as coming from E. Jewett (CARPENTER, 1864:536, 1865:177) and J. G. Cooper (CARPENTER, 1865:177). The still present material of these collections is now in USNM, UCB, or the Redpath Museum, McGill University. However, PALMER (1958) was unable to locate the type material of *Solen rosaceus* in one of these institutions and also not in BMNH (as erroneously stated by OLDROYD, 1925) (PALMER, 1958:25, 115); the material is apparently lost. For nomenclatural stability, a



Explanation of Figures 51 to 59

Figures 51–59. *Solen rostriformis* Dunker. Scale = 10 mm. Figure 51. “San Diego” form. Santo Domingo, outer coast of Baja California, Mexico, leg. C. R. Orcutt, SDNHM 15442. Neotype of *Solen lappeanus* Dunker, 1871. Interior and exterior of both valves. Figure 52. Second specimen of same lot as in Figure 51. Exterior of left valve. Figure 53. “San Diego” form. San Felipe Bay, Baja California, between Playa Alicia and Pete’s Camp, sandbars at edge of low tide, leg. Gemmell, 1964–1975, SDNHM 90140. Exterior of left valve, interior of right valve. Figure 54. “San Diego” form. Newport Bay, California, MCZ 63501, ex E. P. Chace coll. Interior and exterior of left valve. Figure 55. Second specimen of same lot as in Figure 54. Interior and exterior of right valve. Figure 56. “San Diego” form. San Pedro, California, leg. A. N. Lowe, December 1924, MNHN, ex Staadt coll. Interior and exterior of right valve. Figure 57. “La Paz” form. Holotype of *Solen rostriformis* Dunker, 1862. BMNH 19771. Interior and exterior of both valves. Figure 58. “La Paz” form. La Paz, Baja California Sur, Mexico, SDNHM 71460. Exterior of both valves, interior of left valve. Figure 59. Second specimen of same lot as in Figure 58. Exterior of left valve.

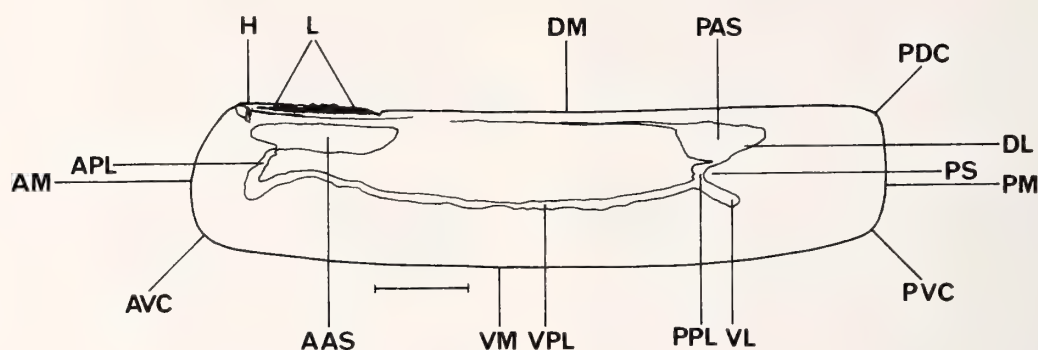


Figure 60

Diagram of *Solen krusensterni* Schrenck (type species of *Ensisolen*). Sukhodol Bight, Ussuri Bay, USSR, on beach, leg. K. A. Lutaenko, 2 April 1989, MNHN. Explanation of shell characters: AAS, anterior adductor scar; AM, anterior margin; APL, anterior pallial line; AVC, anteroventral corner; DL, dorsal limb of pallial sinus (here united with the posterior adductor scar); DM, dorsal margin; H, hinge tooth under the beak; L, ligament; PAS, posterior adductor scar; PDC, posterodorsal corner; PM, posterior margin; PPL, posterior pallial line; PS, pallial sinus; PVC, posteroventral corner; VL, ventral limb of pallial sinus; VM, ventral margin; VPL, ventral pallial line.

neotype is designated here: MNHN, San Pedro, leg. H. N. Lowe, 23 December 1924.

Type locality: "Santa Barbara (Jewett); San Pedro (Cooper)" (CARPENTER, 1865:177), here restricted to San Pedro, California (33°45'N, 118°19'W).

Description: Shell small, up to 57 mm long, elongate, somewhat variable in length-width ratio (4.7-5.5:1), thin and fragile. Dorsal margin straight to very faintly concave, rarely somewhat convex; ventral margin generally distinctly convex, often giving the valves as a whole a slightly curved appearance. Anterior margin well rounded and prominent; posterior third or fourth of the valves tapering, ventrally more than dorsally; posterior margin vertically truncate, with well-rounded corners. Broadest part of the valves in front of the posterior muscle scar. Hinge and ligamental area slightly bent upwards.

Anterior adductor scar elongate, by $\frac{1}{3}$ to $\frac{1}{6}$ longer than

the ligament. Posterior adductor scar above the pallial sinus and united with its dorsal limb. Pallial sinus short and rather narrow, with the innermost point usually in the middle or the lower part, occasionally in the upper part. Distance between innermost point of pallial sinus and posterior margin relative to the total shell length ("pallial sinus ratio"; for diagrams see Figure 60 and COSEL, 1989:204) 1:3.6-4.1. Exterior smooth and glossy, with fine, irregular growth lines.

Valves whitish, with several concentric pale brownish-red zones parallel to the growth lines. Periostracum light olive greenish. Interior light grayish white with the brownish-red zones showing through.

Animal not seen.

Selected measurements with length-width ratio:

57.3 × 10.5 mm Long Beach, SDMNH	5.5 : 1
56.7 × 10.5 mm San Diego, AMNH	5.4 : 1

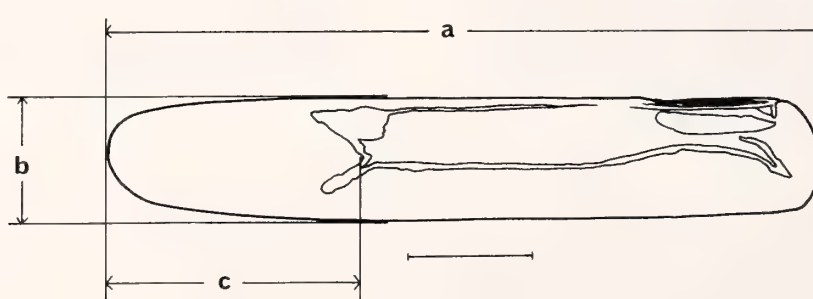
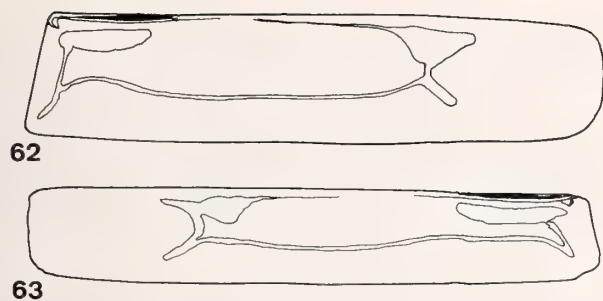


Figure 61

Diagram of *Solen rostriformis* Dunker. Upper Newport Bay, Orange Co., California, LACM 104777. Explanation of shell parameters: a = shell length; b = shell width; a:b = length-width ratio; c = distance from innermost point of the pallial sinus to the posterior margin; c:a = pallial sinus ratio (ratio of the distance between the innermost point of the pallial sinus and the posterior margin to total shell length).



Explanation of Figures 62 to 63

Figures 62 and 63. Examples of *Solen* not belonging to *Ensiosolen*. Figure 62. *Solen vagina* Linné, 1758. Possible syntype, Linnean Society of London. Type species of the genus *Solen*. Note the sharply truncated anterior margin; an anterior furrow is absent; the posterior adductor scar is united with the dorsal limb of the pallial sinus. Figure 63. *Solen sloanii* Gray in Hanley, 1842. The inflexion at the anteroventral corner marks the deep anterior furrow; the posterior adductor scar is situated in front of the pallial sinus.

55.6 × 10.4 mm Long Beach, SDMNH	5.3 : 1
54.1 × 10.3 mm Long Beach, SDMNH	5.3 : 1
52.8 × 10.4 mm Long Beach, SDMNH	5.1 : 1
51.6 × 9.5 mm San Diego, AMNH	5.4 : 1
50.1 × 9.6 mm Long Beach, SDMNH	5.2 : 1
50.0 × 9.7 mm Long Beach, SDMNH	5.2 : 1
47.9 × 9.6 mm San Diego, AMNH	5.0 : 1



Figure 64

Distributions of *Solen rosaceus* (circles) and *Solen gemmelli* Cosel, sp. nov. (squares). The doubtful record from Morro Bay is marked by an empty circle.

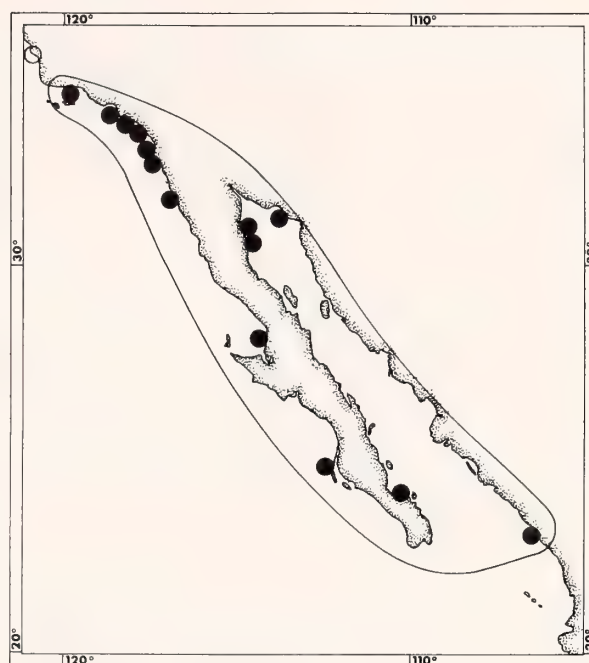


Figure 65

Distribution of *Solen rostriformis*. The doubtful record from Morro Bay is marked by an empty circle.

47.2 × 8.8 mm San Pedro, MCZ	5.4 : 1
44.8 × 8.8 mm San Diego, AMNH	5.1 : 1
44.7 × 9.6 mm San Pedro, MCZ	4.7 : 1
44.4 × 8.7 mm San Pedro (neotype)	5.1 : 1
44.0 × 8.8 mm San Diego, AMNH	5.0 : 1
44.0 × 8.4 mm San Diego, AMNH	5.3 : 1
43.8 × 9.2 mm San Pedro, MCZ	4.8 : 1
35.1 × 7.1 mm San Pedro, MCZ	4.9 : 1
30.0 × 6.0 mm San Pedro, MCZ	5.0 : 1
29.9 × 6.2 mm San Pedro, MCZ	4.8 : 1

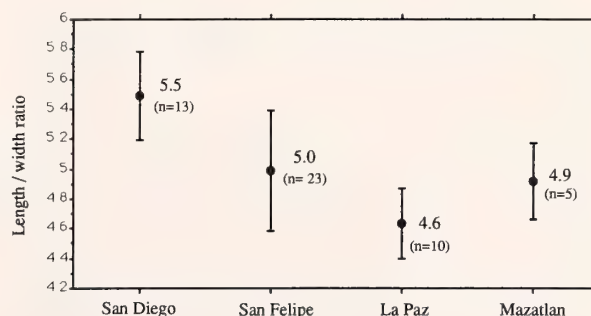


Figure 66

Length-width ratio of *Solen rostriformis* populations from California and the outer coast of northern Baja California ("San Diego"), the San Felipe area in the northern Gulf of California ("San Felipe"), northern to southern Baja California ("La Paz"), and Mazatlan. Bars are 1 SD.

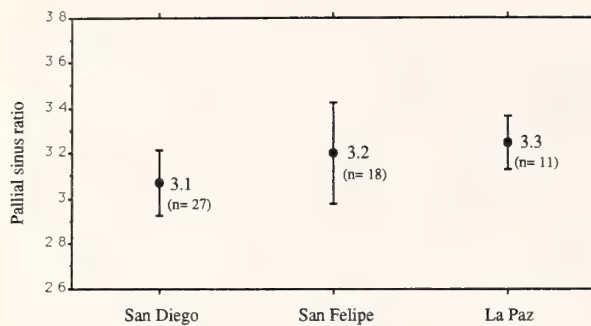


Figure 67

Pallial sinus ratio of *Solen rostriformis* populations from California and the outer coast of northern Baja California ("San Diego"), the San Felipe area in the northern Gulf of California ("San Felipe"), and northern to southern Baja California ("La Paz"). Bars are 1 SD.

Distribution: Restricted to a rather short strip on the California coast. Usually, Santa Barbara (34°N) is given as the northern limit; a mixed lot in ZIM containing both this species and *Solen rostriformis* is labelled "Morro Bay" (35°20'N), but this record needs confirmation. The species goes southward to San Diego (33°N).

Material examined: The neotype; USA, CALIFORNIA: Morro Bay, 1 shell, M. & E. Caruthers, 1937, ZIM; Long Beach, Los Angeles, 7 shells, SDNMH, ex H. N. Lowe coll.; Terminal Beach, Los Angeles, 1 shell, leg. Tremper, AMNH 206948; Terminal Island, Los Angeles, 4 shells, 5 valves, leg. Mrs. W. H. Eshnaur, 28 July 1928, MNHN, ex Staadt coll.; Anaheim Landing, San Pedro Bay, Los Angeles, 5 shells, leg. E. P. Chace, MCZ 67379; San Pedro, Los Angeles, 10 shells (no more details), MCZ 51594, ex E. P. Chace coll.; 5 shells (no more details), MNHN, ex Denis coll.; San Diego, 6 shells, AMNH 26317, ex I. S. Oldroyd coll., 1 shell, AMNH 26307 (specimen figured in EMERSON, 1981:pl. 121, fig. 9).

Biotope: In fine muddy sand in protected bays, from the lower intertidal zone to shallow water, apparently only locally common.

Remarks: This species is characterized by its typical pale brownish-red growth zones in combination with the normally slightly curved shell, the rounded anterior margin, and the rounded-truncated posterior margin (one of the studied specimens had a straight shell, Figure 5). The species closest to *Solen rosaceus* in outline and arrangements of muscle scars and mantle line is *S. tairona* Cosel, 1985, from the Colombian Caribbean coast; however, this South American species is a bit more slender, much smaller, thinner, and virtually translucent. The other close Atlantic species, *S. viridis* Say, 1821, from the U.S. east coast (Rhode Island to Texas) is translucent white (occasionally with a few rose growth lines in southern specimens) and has a pale yellowish green periostracum. The only eastern Pa-

cific species resembling *S. rosaceus* is *S. gemmelli* sp. nov. (see description below). *Solen sicarius*, of which *S. rosaceus* was originally considered a "variety" by Carpenter, is much larger, heavier, and somewhat shorter and broader, with a less rounded posterior margin. This more northern species has a much wider range, from the extreme southeast of Alaska (56°N) (BERNARD, 1983) to north of San Diego (33°N, rare) (BERNARD, 1983); *S. rosaceus* overlaps with it in the greater part of its range.

The type material of *Solen rosaceus* has never been figured. From the brief descriptions ("*Solen* ?var. *rosaceus*. Straight, narrower, longer, smaller; glossy, rosy"—CARPENTER, 1864:638; "*Solen* (?*sicarius*, var.) *rosaceus*. *S. testa* *S. sicario* simili, sed minore; multo angustiore, elongata, recta, extus et intus rosacea; epidermide tenui, valde nitente."—CARPENTER, 1865:177), it is not clear which of the two sympatrically occurring species Carpenter really had before him. From the "similarity" to *S. sicarius* and the "rosy" coloration on the interior and exterior, and in spite of the citation "straight," one could assume that the rather range-restricted California species treated above was concerned (although it is mostly slightly curved), but it is not completely sure. However, the final reason for selecting the neotype of *Solen rosaceus* from this species is nomenclatural: using the name *rosaceus* for this species avoids the introduction of another new name.

Solen (Ensisolen) gemmelli Cosel, sp. nov.

(Figures 8–14, 47–50, 68, 69)

Solen new species A: GEMMELL, MYERS & HERTZ, 1987:57.

Type material: Holotype SDNHM 90139, San Felipe, Golfo de California, Mexico, between Playa Alicia and El Paraiso, on sandbars at low tide mark, leg. Gemmell, between 1965 and 1976. Paratypes: Pete's Camp to Playa Alicia, a coastline of about 50 km, stretching N and S of Bahia San Felipe, 5 specimens (3 partly broken), 3 valves, SDNHM 90139 [new number for paratypes].

Type locality: San Felipe, Golfo de California, Mexico (31°03'N, 114°52'W).

Description: Shell rather small, up to 63 mm long, thin and translucent, very elongate, somewhat variable in outline, slightly curved to occasionally straight, with length-width ratio 5.3–6.3:1. Anterior margin obliquely rounded-truncate, with well-rounded anteroventral corner. Posterior margin vertically truncate, slightly convex, with well-rounded dorsal and ventral corners. Dorsal margin somewhat concave to straight, rarely somewhat convex in its posterior part; ventral margin mostly slightly convex. Hinge and ligamental area faintly to markedly bent upwards.

Anterior adductor scar long and narrow, about ¼ to ½ its length longer than the ligament. Posterior adductor scar united with the pallial sinus and stretching for half of its length above it. Pallial sinus triangular to trapezoid, with

the innermost point mostly in the upper part. Distance between that innermost point and the posterior margin relative to the total shell length 1:3.4–4.0.

Exterior smooth, with faint growth lines and coarser growth stages. Valves entirely white and lacking any coloration, periostracum light yellowish green.

Live or wet preserved animals not seen.

Selected measurements with length–width ratio:

63.0 × 11.1 mm San Felipe (paratype)	5.7 : 1
60.0 × 9.5 mm San Felipe (holotype)	6.3 : 1
57.3 × 9.6 mm San Felipe (paratype)	6.0 : 1
56.5 × 10.6 mm San Felipe (paratype)	5.3 : 1
53.4 × 8.8 mm San Felipe (paratype)	6.1 : 1
49.6 × 8.6 mm San Felipe (paratype)	5.8 : 1
42.2 × 7.5 mm San Felipe (paratype)	6.2 : 1
36.8 × 7.0 mm San Felipe (paratype)	5.3 : 1
26.0 × 4.8 mm San Felipe (paratype)	5.4 : 1

Distribution: At present only known from the San Felipe area, Gulf of California, Pacific coast of Mexico.

Material examined: The type material; MEXICO: 32 km S of San Felipe, Baja California, intertidal, 1 valve, *leg.* Faye B. Howard, April 1957, LACM 104778, *ex* Kana-koff coll.

Etymology: The species is dedicated to Joyce Gemmell, who assembled an extensive marine mollusk collection from the San Felipe area between 1964 and 1975 (GEMMELL *et al.*, 1987) and collected the species here described.

Biotope: In fine sand, at lower intertidal zone and low water mark.

Remarks: This new species is in outline very close to *Solen rosaceus* and *S. tairona*; however, the most conspicuous features that distinguish it from *S. rosaceus* are the complete lack of color and its generally longer and much more slender shell. It is the most slender species of the *rosaceus* group, only *S. tairona* approximates it nearly (5.2:1 for *S. tairona* versus 5.3:1 for the “shortest” *S. (E.) gemmelli*). There are no substantial differences in the curvature of the margins and the muscle impressions; however, the anterior muscle scar and the ventral limb of the pallial sinus in *S. gemmelli* are more prolonged, corresponding to the longer shell. *Solen rostriformis* (see below), which occurs with *S. gemmelli* in the same habitat, is shorter and straight, with a rounded posterior margin, more truncate anterior margin, and a larger distance between the innermost point of pallial sinus and posterior margin.

The southernmost record of *Solen rosaceus* is San Diego, and no record of this species on the outer coast of Baja California is known to me. This leads to the assumption that *S. gemmelli* and *S. rosaceus* might be a pair of allopatric sibling species, the Caribbean and eastern Atlantic counterpart being *S. tairona* in the south and *S. viridis* in the north.

Solen (Ensisolen) rostriformis Dunker, 1862

Solen rostriformis DUNKER, 1862:421.

Solen lappeanus DUNKER, 1871:129–130, pl. 44, fig. 1.

Solen new species B: GEMMELL, MYERS & HERTZ, 1987:57.

S. rosaceus: WEYMOUTH, 1920:50; pl. 15, fig. 3; FITCH, 1953: 76, fig. 42; MCLEAN, 1969:88, fig. 3; HADERLIE & ABBOTT, 1980:385, pl. 124, fig. 15.62; REHDER, 1981: fig. 615, p. 673.

Type material: The holotype of *Solen rostriformis* is in BMNH (No. 19771). The type material of *S. lappeanus* has not been located, either in BMNH or in ZMB, and is apparently missing. For nomenclatural stability, a **neotype** is **designated here**: SDNHM 15442, Santo Domingo, Baja California, *leg.* C. R. Orcutt.

Type locality: *Solen rostriformis*: not given, here selected as La Paz, Baja California Sur, Mexico (24°10'N, 110°17'W). *S. lappeanus*: “Mare Antillarum,” here corrected to Santo Domingo, Baja California, Mexico (28°10'N, 114°08'W).

Description: Shell small to medium-sized, up to 70 mm long, thin and fragile (very large specimens rather solid), elongate, very variable in length–width ratio (4.6–6.0:1), outline and coloration. Dorsal margin straight to faintly convex; ventral margin straight, slightly convex or occasionally even slightly concave in the middle part. Anterior margin more or less obliquely truncated, with rounded ventral corner, posterior margin well-rounded to nearly semicircular. Posterior part weakly to markedly tapering from just in front of or behind the level of the posterior adductor scar. Broadest part of the valves in the middle or behind the middle but usually more or less in front of the posterior adductor scar. Hinge and ligamental area slightly bent dorsally.

Anterior adductor scar elongate, somewhat variable in length, slightly shorter or longer than the ligament. Posterior adductor scar above the pallial sinus and its posterior part united with the dorsal limb of the sinus. Pallial sinus short, with the innermost point mostly at the lower part. Distance between innermost point of the pallial sinus and posterior margin relative to the total shell length somewhat variable but always rather large: 1:2.7–3.6. Exterior with fine irregular growth lines and occasional coarser growth stages.

Valve color varies from entirely white, whitish with rosy hue especially between the anterior adductor scar and the ligament plate or around the scar, slightly brownish pink, uniform pale pink or white to pale pink with occasional more intensively colored growth zones. Periostracum greenish to light brownish green, in very large specimens turning to brown. Interior with same coloration as exterior.

Animal not seen.

Selected measurements with length–width ratio:

69.5 × 13.2 mm Sto. Domingo (neotype of <i>S. lappeanus</i>), SDNHM 15442	5.3 : 1
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68.0 × 13.0 mm	Sto. Domingo, Baja California, SDNHM 15442	5.2 : 1
64.5 × 10.8 mm	Upper Newport Bay, LACM 104777	6.0 : 1
64.4 × 10.7 mm	Upper Newport Bay, LACM 104777	6.0 : 1
63.7 × 11.6 mm	San Diego, MCZ 74369	5.5 : 1
59.8 × 10.6 mm	Santa Barbara, ZMB	5.6 : 1
58.9 × 11.2 mm	Upper Newport Bay, LACM 104777	5.3 : 1
58.4 × 11.6 mm	Bahia San Felipe, SDNHM 90140	5.0 : 1
57.5 × 11.0 mm	San Diego, AMNH 51594	5.2 : 1
56.9 × 12.3 mm	San Felipe, SDNHM 22576	4.6 : 1
55.7 × 10.1 mm	Santa Barbara, ZMB	5.5 : 1
55.5 × 11.8 mm	Holotype of <i>S. rostriformis</i> , BMNH	4.7 : 1
55.5 × 11.1 mm	San Diego, MCZ 140200	5.0 : 1
53.6 × 9.3 mm	40 km S of San Felipe, MCZ 215041	5.8 : 1
51.1 × 10.1 mm	40 km S of San Felipe, MCZ 215041	5.1 : 1
49.6 × 8.7 mm	Tierra del Fuego Isle, SDNHM 54947	5.7 : 1
49.2 × 9.6 mm	Puerto San Carlos, LACM 71-186	5.1 : 1
49.1 × 10.5 mm	Puerto Penasco, AMNH 178035	4.7 : 1
48.2 × 10.4 mm	Mazatlan, CAS 03969	4.6 : 1
46.7 × 8.8 mm	Newport Bay, MCZ 63501	5.3 : 1
46.0 × 8.7 mm	Mazatlan, CAS 03969	5.3 : 1
44.0 × 7.9 mm	Tierra del Fuego Isle, SDNHM 54947	5.6 : 1
42.0 × 9.0 mm	La Paz, SDNHM 71460	4.7 : 1
41.6 × 8.6 mm	La Paz, SDNHM 71460	4.8 : 1
36.7 × 7.5 mm	El Magote, La Paz, LACM 66-29	4.9 : 1
35.8 × 7.4 mm	Estero de Punta Banda, LACM 64-33	4.8 : 1

Distribution: Santa Barbara, California (34°N), southward to Mazatlan, Sinaloa, Mexico (23°N), and throughout the Gulf of California. As in *Solen rosaceus*, the mixed lot from Morro Bay in ZIM might suggest a range extension to the north, but that needs confirmation.

Material examined: USA, CALIFORNIA: Morro Bay, 1 shell, 1 valve, *leg.* M. Caruthers, 1937, ZIM; Santa Barbara, 2 shells, ZMB, *ex* Dunker coll.; Terminal Beach, Los Angeles, 3 valves, AMNH 206948, *ex* Tremper coll.; Terminal Island, Los Angeles, 1 valve, *leg.* Mrs. W. H. Eshnaur, 28 July 1928, MNHN, *ex* Staadt coll.; Newport Bay, Orange Co., 3 shells, *leg.* T. Burch, AMNH 131917;

7 shells, *leg.* E. P. Chace, MCZ 63501; Upper Newport Bay, 7 shells, LACM 104777; San Diego Bay (no more details), 30 shells, MCZ 140200, *ex* Grand Rapids Public Museum; 3 shells, AMNH 51594, *ex* Constable coll.; 1 valve, AMNH 26917, *ex* Oldroyd coll.; San Diego Bay, 9–11 fm., 16 specimens, *leg.* Kofoed & Raymond, 13 July 1901, CAS 039968; San Diego (no more details), 4 shells, 1 valve, MCZ 74369, *ex* Hemphill coll.; 3 shells, MCZ 74370, *ex* Button coll.; 4 shells, MCZ 87121, *ex* Roper coll.; 1 shell, MNHN, *ex* Denis coll.; Tierra del Fuego Isle, Mission Bay, San Diego, 6 shells, *leg.* R. L. Morrison, 11 April 1969, SDNHM 54947; Chula Vista, near San Diego, 1 shell, *leg.* Reed, ZIM; California (no details), 2 × 1 shell, MNHN; MEXICO: Estero de Punta Banda, Baja California, 31°46.6'N, 116°37.3'W, intertidal sand and mudflats, 1 specimen, *leg.* McLean, 20 December 1964, LACM 64-33; Santo Domingo, Baja California, 2 shells, *leg.* C. R. Orcutt, SDNHM 15442, *ex* Baily coll.; Bahia Santa Inez, 1.6 km S of Sto. Domingo Pt., Baja California, 2 shells, *leg.* C. R. Orcutt, SDNHM 15442, *ex* Baily coll.; Bahia Santa Inez, 1.6 km S of Sto. Domingo Pt., Baja California, 1 shell, 1 valve, AMNH 78609; Puerto San Carlos, Bahia Magdalena, Baja California Sur, 24°47.4'N, 112°6.3'W, intertidal sand flat, 3 specimens, *leg.* C. Swift, 3 November 1971, LACM 71-186; La Paz, Baja California Sur (no more details), 5 shells, 2 valves SDNHM 71460; El Magote, La Paz Harbour, 24°10'N, 112°00'W, 1 specimen, *leg.* McLean *et al.*, 11 April 1966, LACM 66-29; 40 km S of San Felipe, Baja California, 7 shells, 1 valve, *leg.* E. P. Chace, March 1957, MCZ 215041; 32 km S of San Felipe, 21 shells, *leg.* F. B. Howard, April 1957, LACM 104778, *ex* Kanakoff coll.; Diggs Point, S of San Felipe, 4 shells, *leg.* E. C. Huffman, June 1934, LACM 104775; 3 shells, *leg.* Huffman, MNHN, *ex* Staadt coll.; San Felipe, in mud just below the surface, 2 specimens, *leg.* M. Rogers, 31 December 1955, LACM 104776; 6 shells, SDNHM 225760, *ex* Lowe coll.; 2 shells, AMNH *ex* Chace coll.; Bahia San Felipe, between Playa Alicia and Pete's Camp, sandbars at edge of low tide, 6 specimens, *leg.* Gemmell, between 1964 and 1975, SDNHM 90140; Bahia Cholla, Puerto Penasco, Sonora, 5 shells, February 1970, AMNH 178035; 1 shell, *leg.* Mrs. R. B. Beck, MNHN, *ex* Staadt coll.; Mazatlan, Sinaloa, *leg.* L. G. Hertlein, 7 valves, 1 fragment, 8 December 1932, CAS IZ039969.

Biotope: In fine sand and fine muddy sand from somewhat above low tide mark to shallow water (10 m).

Remarks: *Solen rostriformis* is distinguished from *S. rosaceus* and *S. gemmelli* by its broader and less curved or straight shell, with truncated anterior and rounded posterior margins, and its white to whitish pink coloration, often with deeper pink in the anterior adductor scar region.

This is an extremely variable species, which tends to develop more or less defined "forms" in the different parts of its distribution. Four are identified below.

Los Angeles and San Diego area (one isolated lot from Santo Domingo, Baja California) ("San Diego" form):

Shells up to about 70 mm long, dorsal margin straight or faintly convex, ventral margin straight or slightly convex, occasionally even somewhat concave; length-width ratio 5.2–5.7:1. Posterior part dorsally and ventrally only slightly tapering; broadest part of the valve mostly behind the middle, more or less near the posterior muscle scar. Distance from the innermost point of the pallial sinus to the posterior margin very large, always more than $\frac{1}{4}$ of shell length, in fully grown specimens to $\frac{1}{3}$ of total shell length (see Table 1). Valves whitish to beige-whitish, anterodorsal often tinged with pale pink and occasionally with a few faint pinkish growth zones. Interior white, mostly with pinkish zone above the anterior adductor scar or a rosy hue around the scar. The two specimens from Santo Domingo are pale brownish rosy with a pink hue above the anterior adductor scar.

West and south coast of Baja California (Estero de Punta Banda, Bahia Magdalena, La Paz) ("Baja California" or "La Paz" form):

Shells to about 55 mm long, with the ventral margin convex over the whole length, dorsal margin straight, occasionally faintly convex but always less than ventral margin; length-width ratio 4.7–5.1:1. Posterior part mostly ventrally tapering from in front of the posterior muscle scar; broadest part of the valve in the middle or slightly before the middle, always in front of the posterior adductor scar. Distance between the innermost point of the pallial sinus and the posterior margin often slightly shorter than in the "San Diego" form (see Table 1). Valves entirely pale rosy or whitish with pink growth zones, rarely entirely white.

Northwestern part of the Gulf of California (San Felipe area) ("San Felipe" form):

Shells up to about 60 mm long, very similar to the San Diego population, but mostly somewhat shorter, with dorsal and ventral margin straight or slightly convex; length-width ratio 4.2–5.8:1. Posterior part slightly tapering dorsally and ventrally as in the San Diego specimens. Broadest part of the valves in the middle or behind the middle, slightly in front of the posterior muscle scar. Distance between the innermost point of the pallial sinus and the posterior margin generally shorter as in the San Diego specimens but occasionally as long (see Table 1). Valves entirely white, sometimes with a pale pinkish point near the beak and rarely with a more extended pinkish hue.

Mazatlan ("Mazatlan" form):

Shells apparently smaller than the more northern specimens (see measurements), dorsal and ventral margin faintly convex; length-width ratio 4.6–5.3:1. Posterior part dorsally and ventrally tapering from the posterior adductor scar onward. Broadest part of the valves just in front of the posterior adductor scar. Distance between the innermost point of the pallial sinus and the posterior margin

Table 1

Comparisons of the length-width ratio and the pallial sinus ratio (the ratio of the innermost point of the pallial sinus to total shell length) in the different morphs of *Solen rostriformis*.

Length-width ratio					
	Ratio	Mean	SD	SE	n
San Diego	5.2–5.7:1	5.485	0.297	0.082	13
San Felipe	4.2–5.8:1	4.983	0.398	0.083	24
La Paz	4.7–5.1:1	4.63	0.231	0.073	10
Mazatlan	4.6–5.3:1	4.92	0.259	0.116	5

Comparisons (* = significant at 95%)

	Mean diff.	Fisher PLSD	Scheffe F-test
San Diego vs. San Felipe	0.502	0.234*	6.188*
San Diego vs. La Paz	0.855	0.284*	12.205*
San Diego vs. Mazatlan	0.565	0.356*	3.404*
San Felipe vs. La Paz	0.353	0.256*	2.562
San Felipe vs. Mazatlan	0.063	0.333	0.048
La Paz vs. Mazatlan	–0.29	0.37	0.829

Pallial sinus ratio

	Ratio	Mean	SD	SE	n
San Diego	1:2.8–3.3	3.07	0.146	0.028	27
San Felipe	1:2.7–3.6	3.2	0.225	0.053	18
La Paz	1:3.1–3.5	3.273	0.135	0.041	11
Mazatlan	1:2.6–3.0	—	—	—	2

Comparison (* = significant at 95%)

	Mean diff.	Fisher PLSD	Scheffe F-test
San Diego vs. San Felipe	–0.134	0.106*	3.009
San Diego vs. La Paz	–0.202	0.125*	5.307*
San Felipe vs. La Paz	–0.073	0.133	0.599

longer than in the Baja California/Gulf of California specimens (ratio of this parameter to total shell length in the two measured specimens 1:2.6 and 3.0). Valves pink with more intense coloration around the anterior adductor scar.

The length-width ratios and pallial sinus ratios of the different populations are summarized in Table 1 and in Figures 66 and 67; a one-way analysis of variance (ANOVA) was run to test for significant differences in the means of the two parameters among the four morphs.

Looking at the studied material of these populations, the trend towards two main "forms" or "lineages" is obvious. A large, straight, usually quite slender, more whitish northern form lives from Santa Barbara, California, to Santo Domingo, Baja California, and is isolated from the outer coast of Baja California, in the extreme northwestern part of the Gulf of California. A smaller, generally somewhat shorter, more rosy southern form with convex ventral margin ranges from Estero de Punta Banda, Baja California, southward to La Paz and perhaps along the east

Table 2

Comparisons of the length-width ratio and the pallial sinus ratio (the ratio of the innermost point of the pallial sinus to total shell length) in *Solen rosaceus*, *S. gemmelli*, and *S. rostriformis*.

Length-width ratio					
	Ratio	Mean	SD	SE	n
<i>S. rosaceus</i>	4.7–5.5:1	5.126	0.233	0.054	19
<i>S. rostriformis</i>	4.6–6.0:1	5.207	0.414	0.081	26
<i>S. gemmelli</i>	5.3–6.3:1	5.714	0.355	0.118	9

Comparison (* = significant at 95%)

	Mean diff.	Fisher PLSD	Scheffe F-test
<i>S. rosaceus</i> vs. <i>S. rostriformis</i>	–0.8	0.213	0.218
<i>S. rosaceus</i> vs. <i>S. gemmelli</i>	–0.588	0.285*	8.57*
<i>S. rostriformis</i> vs. <i>S. gemmelli</i>	–0.507	0.272*	6.992*

Pallial sinus ratio

	Ratio	Mean	SD	SE	n
<i>S. rosaceus</i>	1:3.6–4.1	3.842	0.209	0.045	22
<i>S. rostriformis</i>	1:2.7–3.6	3.152	0.194	0.026	56
<i>S. gemmelli</i>	1:3.4–4.0	3.741	0.212	0.08	7

Comparison (* = significant at 95%)

	Mean diff.	Fisher PLSD	Scheffe F-test
<i>S. rosaceus</i> vs. <i>S. rostriformis</i>	0.691	0.1*	94.922*
<i>S. rosaceus</i> vs. <i>S. gemmelli</i>	0.101	0.172	0.683
<i>S. rostriformis</i> vs. <i>S. gemmelli</i>	–0.59	0.159*	27.255*

coast of the Gulf of California northward. According to the studied material, the two forms seem to overlap between Estero de Punta Banda (31°56'N) and Santo Domingo (28°10'N, 114°08'W) (see below).

The two allopatric populations of the northern ("San Diego" and "San Felipe") form differ slightly but significantly in their length-width ratios and less in their pallial sinus ratios (see Figures 66, 67). ANOVA (length-width ratio: $F = 13.00$; $df = 3, 47$; $P < 0.01$; pallial sinus ratio: $F = 6.32$; $df = 2, 53$; $P < 0.01$) reveals for the difference in length-width ratio of the two populations a significance at the 95% level in the Fisher PLSD test and the Scheffe F-test; the pallial sinus ratios differ significantly (95% level) only in the Fisher PLSD test.

The difference in length-width ratio between the northern "San Diego" population and the southern "La Paz" form is significant at 95% in the Fisher PLSD test and Scheffe F-test; the "La Paz" form and the northern "San Felipe" population, however, differed significantly only in the Fisher PLSD. The difference in the pallial sinus ratio is significant at 95% in the Fisher PLSD and the Scheffe F-test between the "San Diego" and the "La Paz" forms; there is no significance at all in this parameter between

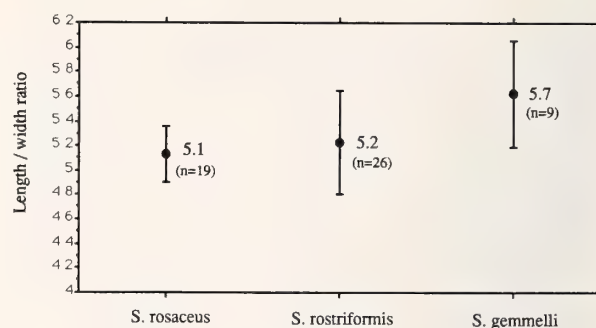


Figure 68

Length-width ratios of *Solen rosaceus*, *S. rostriformis*, and *S. gemmelli*. Bars are 1 SD.

the "La Paz" form and the "San Felipe" population. The "Mazatlan" form, with very few specimens at hand, was included in the length-width ratio analysis only; it showed a significant difference in comparison with the "San Diego" population only.

Intergrades between the different forms seem to be not infrequent: the studied specimen from Estero de Punta Banda has the outline of the southern form but is entirely white. The coloration of the specimens from Mazatlan is like that in the southern "La Paz" form, but these specimens are straight with a long distance between the pallial sinus and the posterior margin, as in the northern "San Diego" form (for the "Mazatlan" form, this parameter could not be included in the ANOVA). Specimens from Bahía Cholla (Puerto Penasco), in the northeastern part of the Gulf of California, are of the "San Felipe" form; however, they might tend slightly to the "La Paz" form (Figures 40–42).

Names are available for both forms: *Solen lappeanus* Dunker, 1871, for the large and straight northern "San Diego-Santo Domingo" variant and *Solen rostriformis* Dunker, 1862, for the shorter, slightly curved southern "La Paz" form.

The holotype of *Solen rostriformis* most closely resembles specimens from the extreme southern part of the range (La Paz): it is very faintly rosy with weak pink growth zones, and the region of and above the anterior adductor scar is more brownish pink, being most intense just behind the beaks.

The original figure of *Solen lappeanus* closely resembles the northern form and is closest to the maximum-size specimens from Santo Domingo, Baja California, with their light brownish interior and dark periostracum. The very shallow depression parallel to the anterior margin mentioned in the description and seen in the original figure is present in many specimens of this variant (e.g., Figures 51, 54). The neotype is hence selected from a lot from Santo Domingo. It corresponds also to the dimensions given for the figured specimen (72 × 11.5 mm).

The two forms are treated here as one species. Analysis

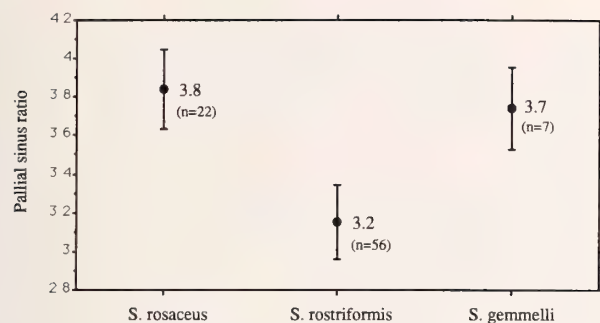


Figure 69

Pallial sinus ratio of *Solen rosaceus*, *S. rostriformis*, and *S. gemmelli*. Bars are 1 SD.

of much more material from many still unworked localities, especially on the east coast of the Gulf of California and the outer coast of Baja California (e.g., the "overlapping area" between Estero de Punta Banda and Santo Domingo), as well as an electrophoretic analysis of all populations and consideration of the fossil record could finally settle the status of these forms.

CONCLUSIONS

"*Solen rosaceus* Carpenter" as understood up to now consists in fact of an allopatric species pair, *S. rosaceus* and *S. gemmelli*, and another very variable species, *S. rostriformis*, which has an intermediate range and overlaps in its distribution with both allopatric species. Table 2 and Figures 68 and 69 compare the length-width ratios and pallial sinus ratios of these three species. The principal differences between the species pair *S. rosaceus*/*S. gemmelli* and *S. rostriformis* are the general shell form, with a usually slightly curved appearance, posterior taper, rounded anterior margin, and truncate posterior margin in *S. rosaceus*/*S. gemmelli*, in combination with a markedly shorter distance between the pallial sinus extremity and the posterior margin in the species pair. *Solen rosaceus* and *S. gemmelli* are themselves clearly distinguished by their different length-width ratios.

For the length-width ratio ($F = 9.215$; $df = 2, 82$; $P < 0.001$), the difference between *Solen gemmelli* on one side and *S. rosaceus* and *S. rostriformis* on the other side is significant at the 95% level in the Fisher PLSD test and the Scheffe F-test. In *S. rosaceus* and *S. rostriformis*, these parameters are not significantly different. In the pallial sinus ratio ($F = 107.53$; $df = 2, 82$; $P < 0.001$), however, *S. rosaceus* and *S. gemmelli* are significantly different from *S. rostriformis* (95% level), whereas there is no significant difference in this parameter between *S. rosaceus* and *S. gemmelli*.

Solen rosaceus and *S. gemmelli* probably have derived from a common ancestor that originally had a continuous distribution. A similar phenomenon is observed in the straight "lappeanus" form of *S. rostriformis*; here, however,

the differences between the "San Diego-Santo Domingo" population and the "San Felipe" population are much smaller and concern mainly the length-width ratio.

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Identification of Monosaccharides in Hydrolyzed *Nautilus* Shell Insoluble Matrix by Gas Chromatography/Mass Spectrometry

by

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Abstract. This study provides the first survey of the monomeric constituents of hydrolyzed *Nautilus pompilius* insoluble shell matrix by gas chromatography/mass spectrometry. Identifying the monomeric constituents of hydrolyzed *Nautilus* insoluble matrix is an important first step in identifying the larger molecules of which the matrix is composed and, ultimately, postulating their function. This study revealed the presence of five monosaccharides not previously reported in the hydrolyzed matrix. These are fucose, xylose, mannose, galactose, and glucose, which together constitute <1% by weight of the matrix. The low concentration of these monosaccharides is not indicative of any structural role for these compounds. Three of these monosaccharides (galactose, mannose, and fucose) are monosaccharide residues often found in glycoproteins.

INTRODUCTION

Interest in identifying organic molecules in the organic matrix of mollusk shells is widespread. This kind of information has been applied to areas as diverse as absolute age dating, stratigraphic correlation, and understanding biomineralizing processes (GRÉGOIRE, 1972; CRENSHAW, 1990; WEHMILLER, 1990). Moreover, studying the organic chemistry of surviving members of groups with an important fossil history, such as *Nautilus*, has added importance because it is the only direct means of understanding the biochemistry of these taxa (LOWENSTAM *et al.*, 1984). Although there has been progress in determining the general types of compounds present in *Nautilus* and other fossil

and Recent shells, the identification of the primary structures of particular macromolecules is in its early stages. The most detailed structural information obtained to date has been the determination of amino acids and amino sugars present after acid-catalyzed organic matrix hydrolysis. This determination often has been done using amino acid analyzers (VOSS-FOUCART, 1968; LOWENSTAM *et al.*, 1984).

In this study, we have employed gas chromatography/mass spectrometry (GC/MS) as a means of surveying the organic chemical composition of the hydrolyzed insoluble organic matrix of *Nautilus pompilius* Linné for compounds other than the amino acids and amino sugars known to be present (VOSS-FOUCART, 1968; WESTBROEK *et al.*, 1979).

This analysis is important because identifying the monomeric constituents of hydrolyzed *Nautilus* matrix may allow for the eventual identification of the larger molecules of which these residues are a part. This, then, could lead to a more complete understanding of the matrix and its function. The organic matrix is divided into two parts, that soluble in aqueous solution (soluble matrix) and that insoluble (insoluble matrix). We investigated the insoluble matrix. Use of GC/MS has allowed us to identify and quantify for the first time five monosaccharides not previously reported in *Nautilus* insoluble matrix.

MATERIALS AND METHODS

Nautilus Shell Material

The material analyzed in this study is the insoluble organic matrix of the shell composing the body chamber of adult *Nautilus pompilius*. The mineralogy of *Nautilus* is wholly aragonitic. Its microstructure has been described by several authors (e.g., MUTVEI, 1972; GRÉGOIRE, 1987; BANDEL, 1990). The outer shell wall has a very thin, inconspicuous periostracum, which is underlain by a layer of granules and spindle-shaped spherulites. The latter grade inward into nearly vertical to slightly reclined, irregular spherulitic prisms, nacreous structure, and then an innermost layer of irregular simple prismatic to fibrous prismatic structure.

Preparation of Shells for Decalcification

Air-dried *Nautilus pompilius* shells with clean-appearing shell surfaces were broken and separated into body chamber fragments. Body chamber fragments then were prepared for decalcification according to the following procedures.

The fragments were soaked in 100% Clorox for 22.5 hr, scrubbed with a nylon brush, and soaked again in Clorox for 0.5 hr. The brushing was necessary to remove from the surfaces of the septa material that did not dissolve in Clorox. The shell fragments were then washed and soaked in distilled water for 0.5 hr and then vigorously agitated in order to complete the washing. After drying, these fragments were broken with a mortar and pestle into pieces approximately 2 cm in diameter.

Decalcification of Shells and Isolation of the Insoluble Matrix

The di-sodium salt (100 g) of ethylenediaminetetraacetic acid (EDTA) was dissolved in 1 L of distilled water. The pH of the solution was adjusted to 7.0 using 1 N sodium hydroxide. Sodium azide (0.2 g), an antibacterial agent, then was added to the solution. Shell fragments (53 g) were placed in the EDTA solution and magnetically stirred for two days, at which time the shell fragments were decalcified, leaving the brownish matrix as an insoluble residue. To ensure complete dissolution, stirring was continued for an additional two days. The stirring then was

halted and the contents of the flask allowed to settle overnight. Approximately 800 mL of the supernatant liquid was decanted. The remaining EDTA solution and suspended material (insoluble matrix fragments) were transferred to 50-mL centrifuge tubes and the material centrifuged until the organic matrix collected into a pellet at the bottom of the tube. The supernatant liquid was removed by pipetting and the pellet was shaken with distilled water. The suspension was centrifuged and the supernatant liquid again removed. This washing process was repeated twice. The centrifuge tubes then were placed in a vacuum desiccator and evacuated using a mechanical pump (ca. 0.1 torr) for 2 hr. The matrix then was left under vacuum in a desiccator containing calcium chloride.

Insoluble Matrix Hydrolysis, Derivatization, Analysis, and Quantification

The dry insoluble matrix was heated with 4.0 mL of 4 N trifluoroacetic acid for 4 hr at 120°C in a sealed tube and thus hydrolyzed (cf. NESSER & SCHWEIZER, 1984). The volatile material was removed under reduced pressure and the residue was heated at 80°C for 15 min in a mixture of pyridine (1.0 mL) and bis(trimethylsilyl)trifluoroacetamide (BSTFA) (0.4 mL) containing a known amount of mannitol as an internal standard. Treatment with BSTFA created trimethylsilylated derivatives of matrix compounds and allowed for their analysis by GC/MS. Analysis was performed using a Finnigan TSQ 45 mass spectrometer operating in positive ion Q1 only mode (source temperature = 120°C, source pressure = 0.03 torr, emission current = 0.3 ma, electron energy = 75 eV). Samples were introduced via the gas chromatograph using a 30 m × 0.25 mm Hewlett-Packard HP-5 ultra performance capillary column operating in the unsplit mode (He pressure = 10 psi, injector temperature = 230°C). The column temperature was maintained initially at 60°C for 1 min and then increased at 10°C/min to a temperature of 150°C. The temperature was held at 150°C for 5 min, then ramped to a final temperature of 280°C at a rate of 2.5°C/min. The temperature was held at this point for an additional 20 min. Compound identification was performed by comparison of both mass spectra and retention times to those obtained from authentic samples.

A standard solution containing known amounts of 10 sugars and mannitol, as an internal standard, was derivatized according to the procedures described above for matrix analysis. Quantification was accomplished by comparing peak areas from the matrix sample with those from the standard solution, and then comparing these peaks to those of the internal standard in light of appropriate response factors.

RESULTS

Five monosaccharides were identified in the form of silylated derivatives in the matrix after hydrolysis and are listed in Table 1. Clearly, the amount of carbohydrate containing

Table 1

Sugar analysis. Monosaccharides in hydrolyzed *Nautilus pompilius* shell insoluble matrix, by gas chromatography/mass spectrometry.

Compound	Weight %	Mole %	Weight % of total sample
Fucose	4.1	4.5	0.018
Xylose	6.1	7.3	0.026
Mannose	25.3	24.9	0.11
Galactose	12.8	12.6	0.054
Glucose	51.7	50.8	0.22

% weight sugars of the total sample = 0.428%.

material present in the insoluble matrix which leads to these sugars is small (<1%). It is a small enough amount to raise the possibility that the carbohydrates may have come from bits of organic matter that were not removed from the shell during the cleaning process. This possibility certainly remains; however, when a second group of shells was cleaned and decalcified by a different person working in a different laboratory, the same sugars were found in the same amounts (after hydrolysis and derivatization). These experiments, taken together, suggest that the sugars listed in Table 1 are a part of the insoluble matrix. This represents the first evidence that these simple sugars are part of the complex macromolecules of which the matrix is composed. Certainly their function at present is unclear; however it seems reasonable that their presence in such low concentrations is not indicative of any structural role for these compounds.

In addition to the monosaccharides found in the matrix, the following ones were also derivatized with BSTFA and analyzed as standards: talose, arabinose, altrose, ribose, rhamnose, and lyxose. Because the derivatives of these sugars were readily detected by GC/MS in standards but not in matrix samples, it is unlikely that they are present in *Nautilus pompilius* insoluble matrix at detectable levels.

Of the five monosaccharides detected, three of them (galactose, mannose, and fucose) are important monosaccharide constituents of glycoproteins (MONTGOMERY, 1970). Montgomery also reports that the two other important carbohydrate constituents of glycoproteins are the amino sugars glucosamine and galactosamine. In addition to the sugars reported above, we also detected the amino sugar glucosamine when we hydrolyzed the insoluble matrix with HCl, as have several previous workers (*e.g.*, VOSS-FOUCART, 1968; LOWENSTAM *et al.*, 1984). While it is generally assumed that much of the glucosamine in mollusk insoluble matrix is in the form of chitin, our results suggest that in addition to studying insoluble matrix carbohydrates in terms of their relationship to chitin, it may also be interesting to investigate the possibility of their being related to a thus far unreported glycoprotein fraction of *Nautilus pompilius* insoluble matrix. Although the study of glycoproteins in mollusk matrix is in its infancy, there

is some evidence of glycoproteinaceous material being present in mollusk matrix and the matrices of other calcium carbonate secreting invertebrates (CRENSHAW, 1972; LOWENSTAM & WEINER, 1989; COLLINS *et al.*, 1991).

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First Study on the Ecology of *Sepia australis* in the Southern Benguela Ecosystem

by

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Abstract. *Sepia australis* is most abundant in the eastern South Atlantic between Luderitz and St. Helena Bay (about 27–33°S in 100–200 m). There seems to be no link between the variation in abundance of *S. australis* and that of its most important predator, the shallow-water Cape hake, *Merluccius capensis*. The variations in abundance of *S. australis* and one of its most important prey species, the stomatopod crustacean *Pterygosquilla armata capensis*, show simultaneous changes, suggesting that both species respond to the same environmental factors.

Mantle length, total weight, gonad weight, and sex ratio of *Sepia australis* vary from year to year and by region off the west coast of southern Africa. Animals from the south coast (eastward of Cape Point) were very different: length-weight relationships were found to be similar in slope and intercept for both sexes and within each sex between years and regions off the west coast, but different for the south coast.

INTRODUCTION

Sepia australis is one of the most common sepiids in the Benguela ecosystem of southern Africa (in this instance from Luderitz to Agulhas Bank, Figure 1; for definitions and geographic boundaries see SHANNON, 1985). It is particularly abundant off the west coast of southern Africa (Figure 1), as indicated by its frequent occurrence in bottom trawls (SANCHEZ & VILLANUEVA, 1989, 1991; LIPINSKI *et al.*, 1991) and the abundance of its cuttlebones on some of the South African beaches (ROELEVELD, 1972: 231). *Sepia australis* is a small cephalopod with a maximum

dorsal mantle length (ML) slightly above 80 mm. Little is known about this species other than its systematic position and distribution range; its importance in the ecosystem is only now being assessed (LIPINSKI *et al.*, 1991, and unpublished data; Roeleveld *et al.*, unpublished data). The species has a known distribution range in southern African waters from southern Namibia (ca. 27°S) to about Rame Head (31°30'S 29°20'E) on the south coast (ADAM & REES, 1966:145; ROELEVELD, 1972:228; SANCHEZ & VILLANUEVA, 1989, 1991; LIPINSKI *et al.*, 1991; Roeleveld *et al.*, unpublished data) and has also been reported from the Red Sea (a single doubtful record in ROCHEBRUNE [1884] repeated by ADAM [1942, 1959]). Its known vertical distribution is 2–457 m (ADAM & REES, 1966:145) but it occurs primarily in the upper 200 m (ROELEVELD, 1972:

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277). The species was reported from southern Namibia only recently, with a center of abundance at 28–30°S in 75–250 m of water and a second, smaller center at 27°S in 150–300 m; its absence off northern Namibia was attributed to the anoxic conditions and narrow continental shelf (SANCHEZ & VILLANUEVA, 1989).

Sepia australis has been caught by the R/S *Africana* in the course of regular biomass surveys conducted by the Sea Fisheries Research Institute off both the west coast and the south coast of South Africa. In 1986 the abundance of *S. australis* was merely estimated for catch records but during the latter part of the survey in January 1987 this species was found to form a significant part of the diet of the shallow-water Cape hake (*Merluccius capensis*) (LIPINSKI *et al.*, in press). Since then, catch data for *S. australis* have been more carefully monitored (Augustyn *et al.*, unpublished data) and extensive biological data, part of which form the basis for this study, have been collected. There is no fisheries-related data base, however, because this species is not fished commercially.

Sepia australis has recently been found widely distributed along the south coast of southern Africa (east of Cape Point; Figure 1). It was shown to be an important species on the Agulhas Bank (Roeleveld *et al.*, unpublished data), where it was found to be primarily a cold-water species, most abundant at bottom-water temperatures of 10–11°C. This agrees with the observation that the abundance of *S. australis* is higher off the west coast than off the south coast (Augustyn *et al.*, unpublished data).

This study presents a first assessment of the biology of *Sepia australis* off the west coast of South Africa, in the southern Benguela ecosystem (Orange River to Cape Agulhas). The distribution, abundance, length/weight relationship, distribution of maturity stages, mean gonad weights, and sex ratio of *S. australis* are described for the first two detailed surveys of the species, in the northern region in 1987 and all three regions in 1988 (Figure 1). Results of the feeding analysis of these samples are described elsewhere (LIPINSKI *et al.*, 1991).

MATERIALS AND METHODS

The biomass surveys of the Sea Fisheries Research Institute are conducted by the R/S *Africana*, usually twice yearly off the west coast of South Africa and once yearly off the south coast. The west coast survey encompasses the southern Benguela ecosystem and extends from the Orange River mouth (ca. 29°S 16°E) to the Agulhas Bank (Figure 1). The south coast survey extends from Cape Agulhas (20°E) to Port Alfred (27°E) (Figure 1). These surveys consist primarily of half-hour bottom trawls during daylight, made in 1.5 × 1.5 m squares selected by the stratified semirandom method (ICSEAF, 1984; PAYNE *et al.*, 1985) and are continuing.

All specimens were collected with a 54-m German otter trawl with 1500-kg polyvalent doors, sampling on the seabed in depths of 50–500 m. Effective mesh size in the cod

end was 27.5 mm (using a pilchard liner). For each trawl, all components of the catch were sorted and weighed; key species such as hake, kingklip, monkfish, and squid were measured and subjected to biological analyses (length, weight, sex, maturity stage, stomach contents, *etc.*).

Sepia australis catch data have been recorded in the course of these biomass surveys since 1986, in depths to 345 m, though data for the first year (January and July 1986) are only estimates and should be treated with caution. The actual weight of *S. australis* caught was recorded from the latter part of the survey (the northern region) in January 1987 and in all subsequent surveys. Almost all *S. australis* catches were made in the 0–209 m depth stratum, and only these data were further analyzed.

Two species that show important interaction with *Sepia australis* are the shallow-water Cape hake (*Merluccius capensis*), one of the sepiid's main predators, and the stomatopod crustacean *Pterygosquilla armata capensis*, one of its two main prey species (LIPINSKI *et al.*, 1991). Only limited information is available for the other main prey species of *S. australis*, the sternoptychid lightfish *Maurolicus muelleri* (HULLEY & PROSCH, 1987; ARMSTRONG & PROSCH, 1991).

The shallow-water Cape hake (*Merluccius capensis*) is not only one of the most important species in the Benguela ecosystem (both ecologically and commercially) but also one of the most important predators in the 0–209 m depth zone between northern Namibia and Cape Columbine (PAYNE *et al.*, 1985, 1986, 1987, 1988, 1989). The geographical distribution of *M. capensis* overlaps that of *Sepia australis* in the area investigated (PAYNE *et al.*, 1985, 1986, 1987, 1988, 1989) and *S. australis* is both a competitor and a prey item of the shallow-water hake. *Sepia australis* also forms a link in the food chain between the mesopelagic *Maurolicus muelleri*, which is consumed by small- and medium-sized hake only (PAYNE *et al.*, 1987), and large hake, which take *S. australis* but not *M. muelleri* (LIPINSKI *et al.*, 1991).

Relatively good data are available on the abundance of the stomatopod *Pterygosquilla armata capensis* (GRIFFITHS & BLAINE, 1988; ABELLO & MACPHERSON, 1990). Therefore, we attempted to compare the abundance of *Sepia australis* with that of *Merluccius capensis* and of *P. armata capensis* caught in the same depth stratum (0–209 m). The abundance indices (as catch per standardized trawl) for *S. australis*, *M. capensis*, and *P. a. capensis* were back-calculated for all R/S *Africana* benthic biomass surveys (both west coast and south coast) for the years 1986–1990. The abundance of *S. australis* before January 1987 was roughly estimated (see above). Data from January 1989 were incomplete and are not included; during the latter survey, the data collected for *S. australis* and *P. a. capensis* were inadequate, because only 16 trawls could be made in the 0–209 m depth zone. *Pterygosquilla a. capensis* was not caught in any of the three south coast biomass surveys discussed here.

For each survey the mean catch per trawl was calculated for all three species under consideration (Table 1). The

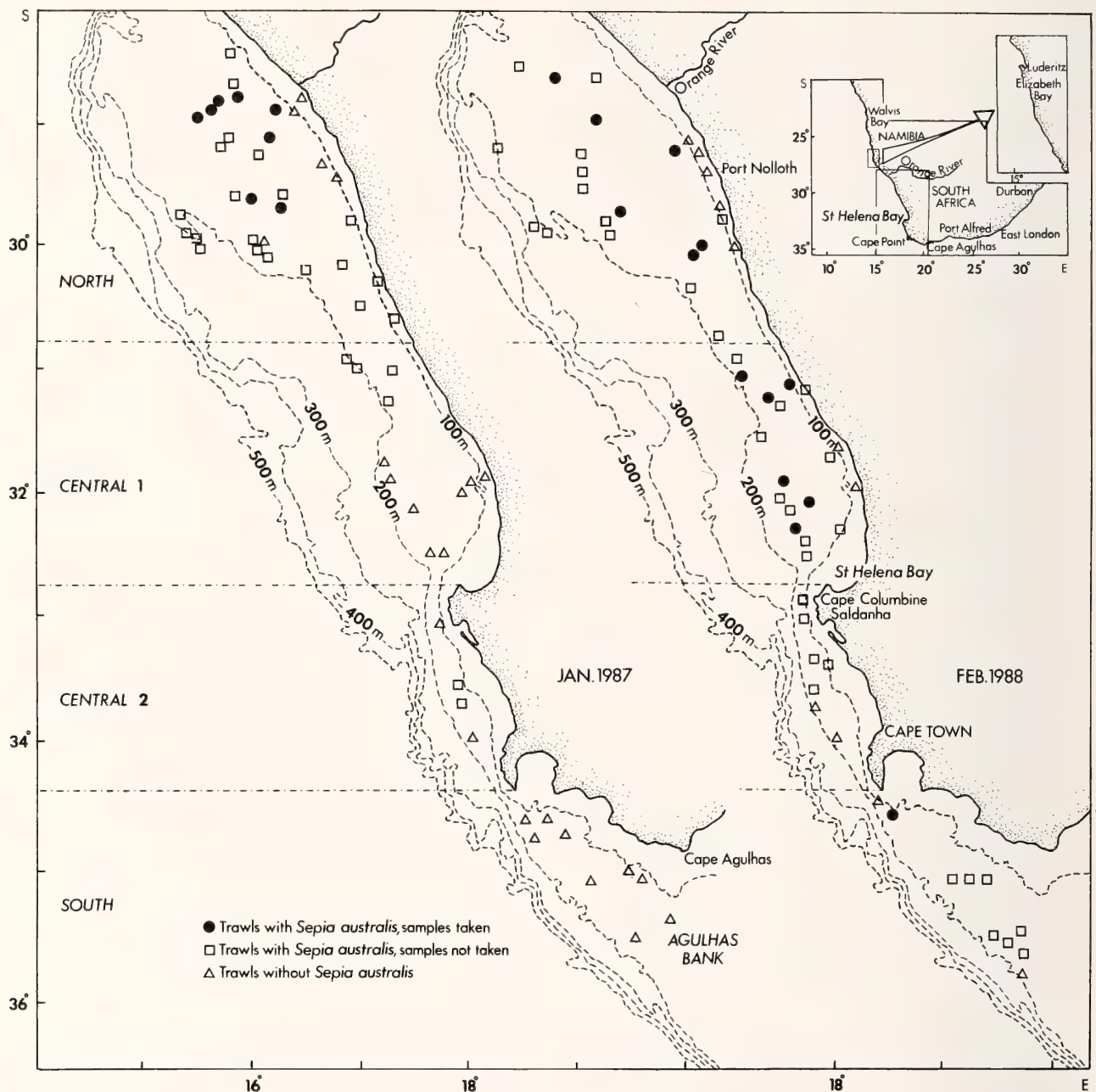


Figure 1

South African west coast biomass survey sampling area, from the Orange River mouth to Cape Agulhas, and localities of stations from which *Sepia australis* samples were collected for biological analysis 22–28 January 1987 and 5–23 February 1988 (closed circles). Stations at which *S. australis* was collected were grouped into northern, central (1 and 2), and southern regions, bounded by broken lines.

mean number of animals per trawl was calculated from the mean individual weight for each species. For *Sepia australis* the mean individual weight was 20.4 g, calculated from regional means for 1987 and 1988 (Table 2). For *Pterygosquilla a. capensis* the mean weight was 11.9 g, calculated from data of GRIFFITHS & BLAINE (1988). The

actual number and total weight of hake for each trawl were determined as part of the routine procedure in these surveys (PAYNE *et al.*, 1985).

The biological analysis is based on specimens collected in the northern region between 22 and 28 January 1987 (Figure 1 left, closed circles: 129 specimens from 9 stations)

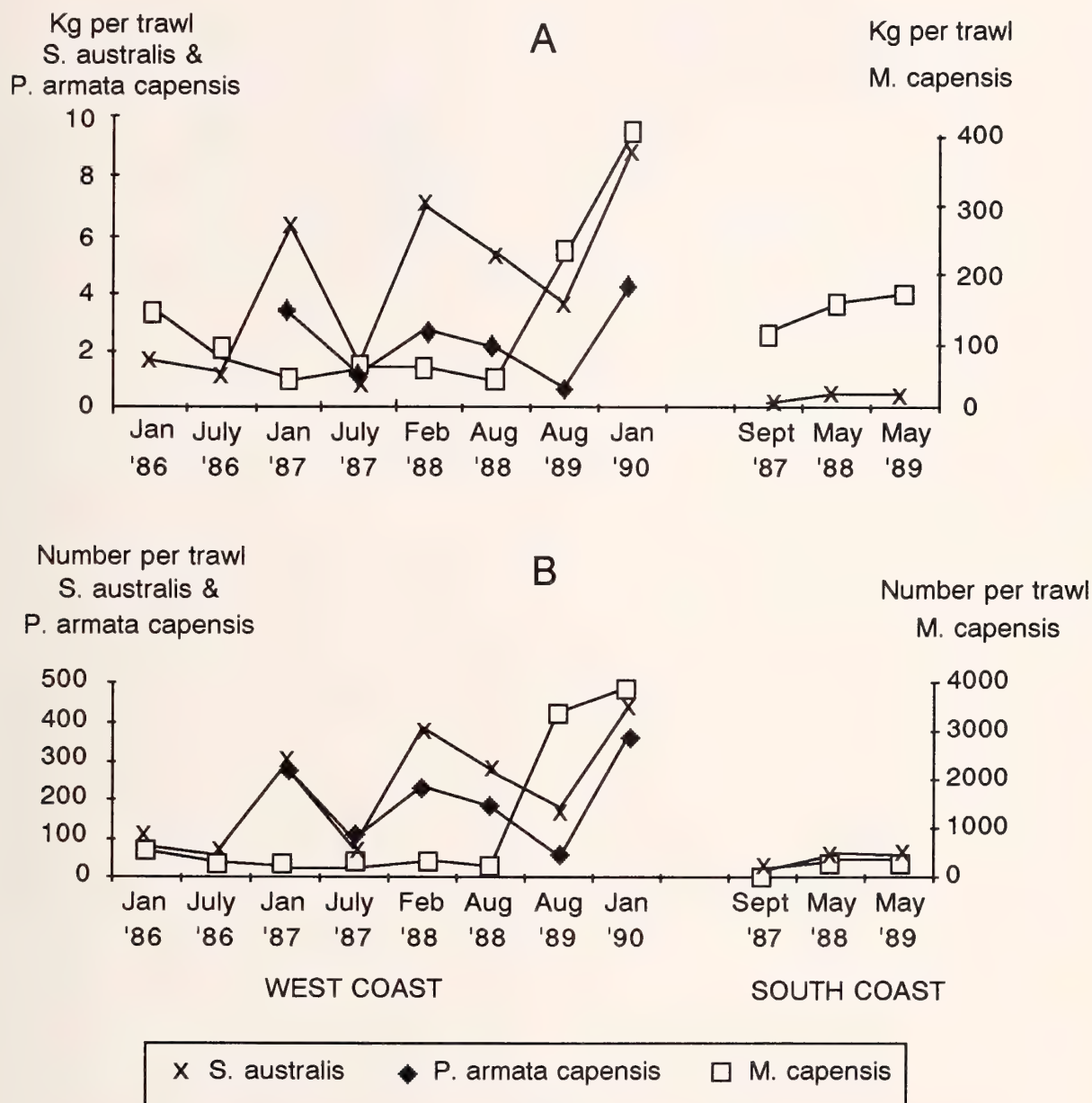


Figure 2

Abundance of *Sepia australis*, *Merluccius capensis*, and *Pterygosquilla armata capensis* in southern African waters. Abundance in mean kg/haul (A) and in mean number of individuals/haul (B) for each survey off the west coast (see text), sampled in summer (January–February) and winter (July–August) and south coast (see text) in spring or autumn (September or May) in 1986–1990. Data for *P. armata capensis* were not collected in 1986; this species was absent in south coast surveys. Variance is not given to simplify the drawings; it does not affect the comparisons of relative abundance.

and throughout the survey between 5 and 23 February 1988 (Figure 1 right, closed circles: 1150 specimens from 12 stations). These stations may conveniently be grouped into the northern, central 1, central 2, and southern regions, as indicated in Figure 1. The boundary between the northern and central 1 regions is arbitrary. There are no pro-

found oceanographic differences between these regions. On the other hand, the oceanography and shelf morphology of the two central regions differ substantially (SHANNON, 1985), and the borderline between them at Cape Columbine reflects real differences. Unfortunately, no samples of *Sepia australis* were collected in the central 2 region.

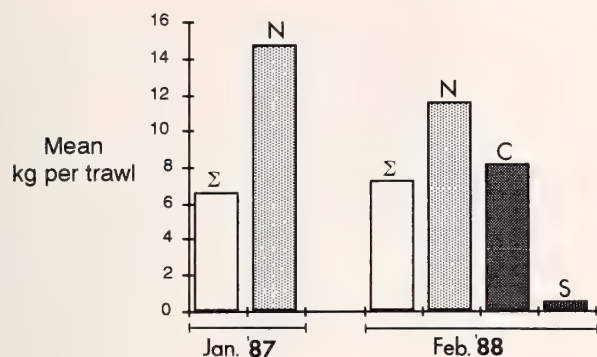


Figure 3

Comparison of abundance of *Sepia australis* off the west coast by region and for the entire survey in each of two summer surveys (1987 and 1988). Sigma—all trawls in the entire survey (up to 209 m); N, C, S—all trawls in northern, central 1, and southern regions, respectively (up to 209 m).

The borderline between the central 2 and southern regions lies at Cape Point (Figure 2). Oceanographically the southern region belongs to the south coast, and the borderline between these regions also reflects real differences (SHANNON, 1985).

Subsamples of *Sepia australis* for biological analysis were frozen immediately after capture and processed in the laboratory. Subsamples contained up to several hundred individuals taken randomly from the sample (*i.e.*, the whole catch per station per species). Biological analysis consisted of determination of dorsal mantle length (to the nearest millimeter), sex and maturity stage (according to a simplified version [ROELEVELD & LILTVED, 1985] of the universal maturity scale for squids [LIPINSKI, 1979]), total weight, gonad weight, and weight of stomach contents

(results of stomach contents analysis were presented by LIPINSKI *et al.*, 1991).

RESULTS

Abundance

The most northerly station at which *Sepia australis* was caught during the west coast biomass surveys was at 27°58.8'S, 14°57.6'E (R/S *Africana* station E46, 190 m, 24 January 1989). During these surveys the species was found at a maximum depth of 345 m, the depth range of main abundance being 140–190 m. Mean catches per trawl of *S. australis* from nine west coast surveys and three south coast surveys in South African waters (Figure 2A, B) show considerable fluctuation, particularly off the west coast. The abundance off the south coast is more regular (Lipinski, unpublished data) but also much lower, by an order of magnitude, than off the west coast (Table 1). *Sepia australis* was generally more abundant in summer than in winter except in 1988 (Figure 2A, B). This general pattern was confirmed by the results of biomass calculations (Augstyn *et al.*, unpublished data).

In comparison with the shallow-water hake (*Merluccius capensis*), the most important fish species in the ecosystem in the 0–209 m depth stratum, the abundance of *Sepia australis* was sometimes higher, as regards to numbers (Figure 2B), since *S. australis* is small and *M. capensis* attains a large size. Compared with the stomatopod *Pterygosquilla armata capensis*, one of its most important prey species, *S. australis* was more abundant both by weight and by numbers (Figure 2A, B).

A comparison of variations in the abundance of *Sepia australis*, *Merluccius capensis* and *Pterygosquilla a. capensis* show interesting trends (Figure 2A, B) that will be checked when a longer time series has accumulated. Available data

Table 2

Sepia australis mean mantle lengths (ML), total weights (TW), with standard deviations (SD), and sex ratio, by year and region off the west coast (see Figure 1).

Area Month, year	Northern Jan. 1987	Northern Feb. 1988	Central Feb. 1988	Southern Feb. 1988	Total
Males (M)					
<i>n</i>	58	167	299	41	565
mean ML ± SD	61.24 ± 6.46	53.56 ± 6.60	55.52 ± 7.01	50.02 ± 4.17	
mean TW ± SD	20.49 ± 5.02	15.49 ± 4.88	17.17 ± 5.34	11.63 ± 2.27	
Females (F)					
<i>n</i>	71	234	373	38	716
mean ML ± SD	65.61 ± 7.78	58.37 ± 7.82	60.43 ± 9.13	54.82 ± 4.96	
mean TW ± SD	24.86 ± 7.15	19.84 ± 6.50	22.62 ± 8.34	15.33 ± 4.26	
Sexes combined					
<i>n</i>	129	401	672	79	1281
mean ML ± SD	63.64 ± 7.51	56.37 ± 7.65	58.25 ± 8.60	52.33 ± 5.14	
mean TW ± SD	22.90 ± 6.63	18.03 ± 6.20	20.20 ± 7.66	13.41 ± 3.84	
Sex ratio, M:F	1:1.22	1:1.40	1:1.25	1:0.93	1:1.27

Table 3

Comparison by *t*-test of *Sepia australis* mean mantle length (ML) and total weight (TW) from Table 2, independent samples by year and region off the west coast (see Figure 1). df, degrees of freedom; *P*, the probability that the regions do not differ significantly.

	Northern Jan. 1987 vs. Northern Jan. 1988			Northern Jan. 1987 vs. Central Feb. 1988			Northern Feb. 1988 vs. Central Feb. 1988			Northern Feb. 1988 vs. Southern Feb. 1988			Central Feb. 1988 vs. Southern Feb. 1988		
	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>
Males															
mean ML	7.68	223	<0.005	5.76	355	<0.001	9.77	97	<0.001	2.95	464	<0.01	3.27	206	<0.001
mean TW	6.67	223	<0.005	4.37	355	<0.001	10.55	97	<0.001	3.36	464	<0.001	4.93	206	<0.001
Females															
mean ML	6.84	303	<0.005	4.48	442	<0.001	7.74	107	<0.001	2.86	605	<0.01	2.71	270	<0.01
mean TW	5.57	303	<0.005	2.12	442	<0.05	7.48	107	<0.001	4.34	605	<0.001	4.13	270	<0.001
Sexes combined															
mean ML	9.43	528	<0.005	6.65	799	<0.001	11.80	206	<0.001	3.61	1071	<0.001	4.50	478	<0.001
mean TW	7.63	528	<0.005	3.74	799	<0.001	11.58	206	<0.001	4.81	1071	<0.001	6.38	478	<0.001

(Figure 2A, B) suggest that variation in hake abundance is not linked to those of *S. australis* or *P. a. capensis*; when the last mentioned two species are scarce, hake can apparently switch easily to other prey species. Nor does the abundance of *S. australis* seem to be influenced by that of hake. On the other hand, changes in the numbers of *P. a. capensis* seem to run parallel with those of *S. australis*.

In both 1987 and 1988, the abundance of *Sepia australis* off the west coast varied greatly among regions (Figure 3). In the southern region the mean catch per trawl was similar to those off the rest of the south coast (Table 1), whereas in the central 1 and northern regions the abundance was much higher (Figure 3), especially in the northern region.

To explore further the relationship between the abundance of *Sepia australis* and that of hake and stomatopods, the number of times that increases and decreases in occurrences were in the same or opposite directions (Figure 2A, B) was counted. The results were as follows:

		<i>Sepia australis</i>		<i>P</i>
		increase	decrease	
Hake	increase	2	1	<i>P</i> = 0.5
	decrease	1	2	
Stomatopods	increase	3	0	<i>P</i> = 0.05
	decrease	0	3	

The Fisher Exact Probability Test for a 2×2 contingency table was used to examine these relationships. For hake the relationship was not significant ($P = 0.50$) but it was significant for stomatopods ($P = 0.05$).

Population Structure

In all surveys, female *Sepia australis* were larger and heavier than males and hence showed greater variation about the mean (*i.e.*, larger standard deviation). Dorsal mantle length (ML) and total weight showed large variations from year to year (Tables 2, 3). In the northern region, differences of 7.27 mm in mean ML and 4.87 g in mean weight (both sexes combined) were recorded in successive years for the same season. Within one year (1988) the ML and total weight of *S. australis* in the central 1 region were significantly greater than in the northern and southern regions (Table 3).

The length-weight relationships (Figure 4) were found to be similar for both sexes and within each sex between years and regions, except in the southern region in 1988. The length-weight relationships for *Sepia australis* in the southern region had a somewhat different intercept and slope for both males (4.6×10^{-3} g and 2.00 g mm⁻¹, respectively) and females (1.3×10^{-3} g and 2.34 g mm⁻¹) than in the northern and central 1 regions in both years (males: 1.1 – 1.3×10^{-3} g and 2.36 – 2.38 g mm⁻¹; females: 0.76 – 0.91×10^{-3} g and 2.44 – 2.48 g mm⁻¹, respectively). The animals in the southern region were also smaller than in the other regions (see above). The lower correlation coefficients in the southern region are probably due primarily to the smaller sample size.

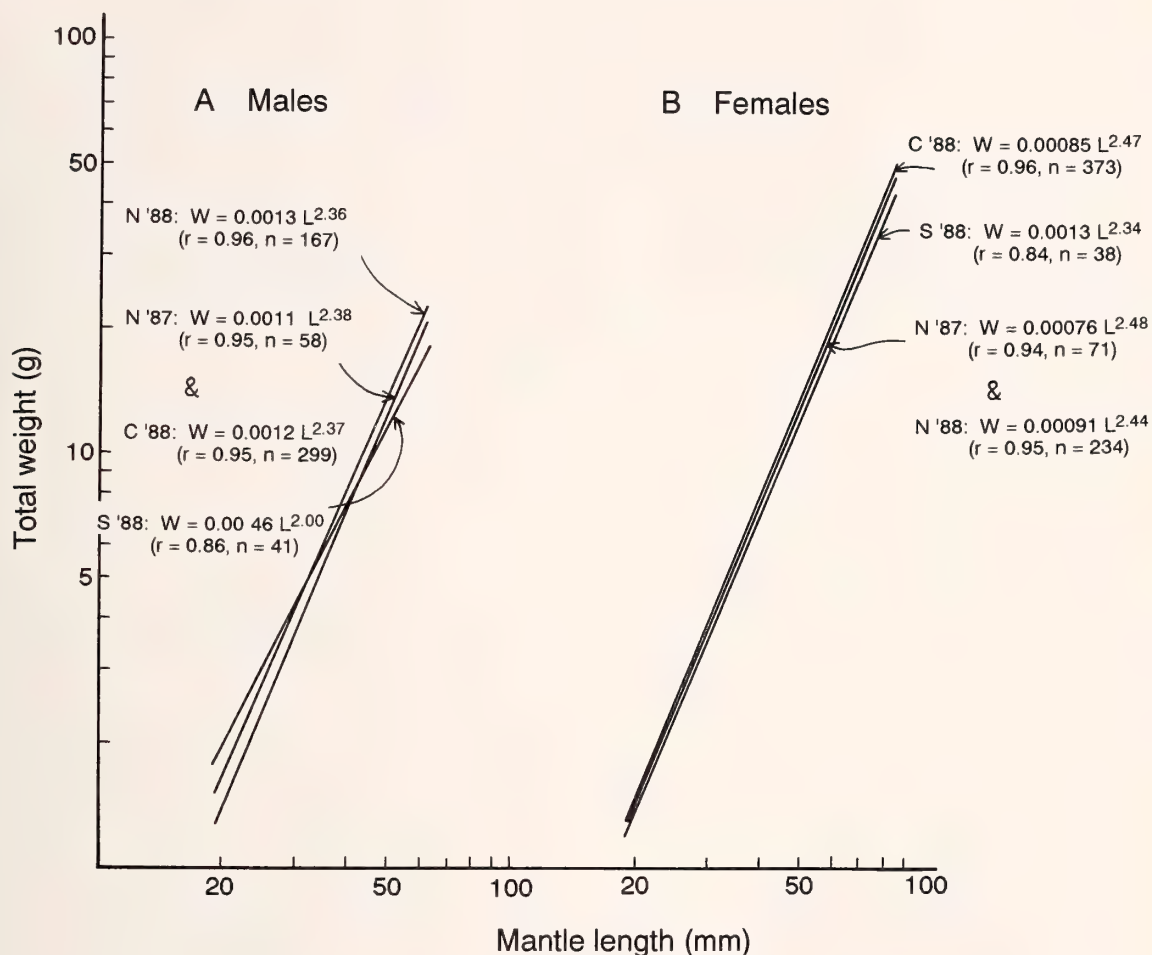


Figure 4

Sepia australis length-weight relationships by year and by region off the west coast in summer 1987 and 1988: Male (A) and female (B) regression lines are virtually the same but have been plotted separately to facilitate comparison among regions; appended to the regression lines are the values for each slope and intercept in the relationship $W = aL^b$ and the correlation coefficient (r) and sample size (n). N, C, S—north, central 1, and southern region, respectively; W is weight in g; L is length in mm.

The distribution of maturity stages varied between years and regions (Figure 5). In the northern region in January 1987, most of the males (56.9%) and females (73.2%) were mature, whereas in February 1988 most animals were completely immature (56.9% and 77.8%, respectively). Mature and maturing males and females were generally bigger than immature animals and there were always slightly more females present than males, except in the southern region, where most of the animals were immature and the sex ratio was about 1:1 (Table 2). In the central 1 region the proportion between mature and immature males was close to parity; there were, however, considerably more immature females.

Mean gonad weights for the different sexes and maturity stages are presented in Figure 6. In the northern region in January 1987, the mean gonad weight for maturity stages II and III was about the same and considerably bigger than for stage I in both sexes. In February 1988,

the mean gonad weight showed a more regular increase in weight from stage I to III in both sexes in all three regions, although the mean gonad weight for stage II was somewhat higher in the central 1 region and there were no fully mature animals of either sex in the southern region. This is in agreement with the observation that in the northern region most of the animals were fully mature or almost so in 1987, whereas in 1988 the animals with the most developed reproductive systems were in the central region, where most of the males and almost half the females were fully mature and stage II animals had somewhat larger gonads (Figures 5, 6).

DISCUSSION

Abundance

Our results confirm that the northern boundary of the distribution range of *Sepia australis* off the west coast of

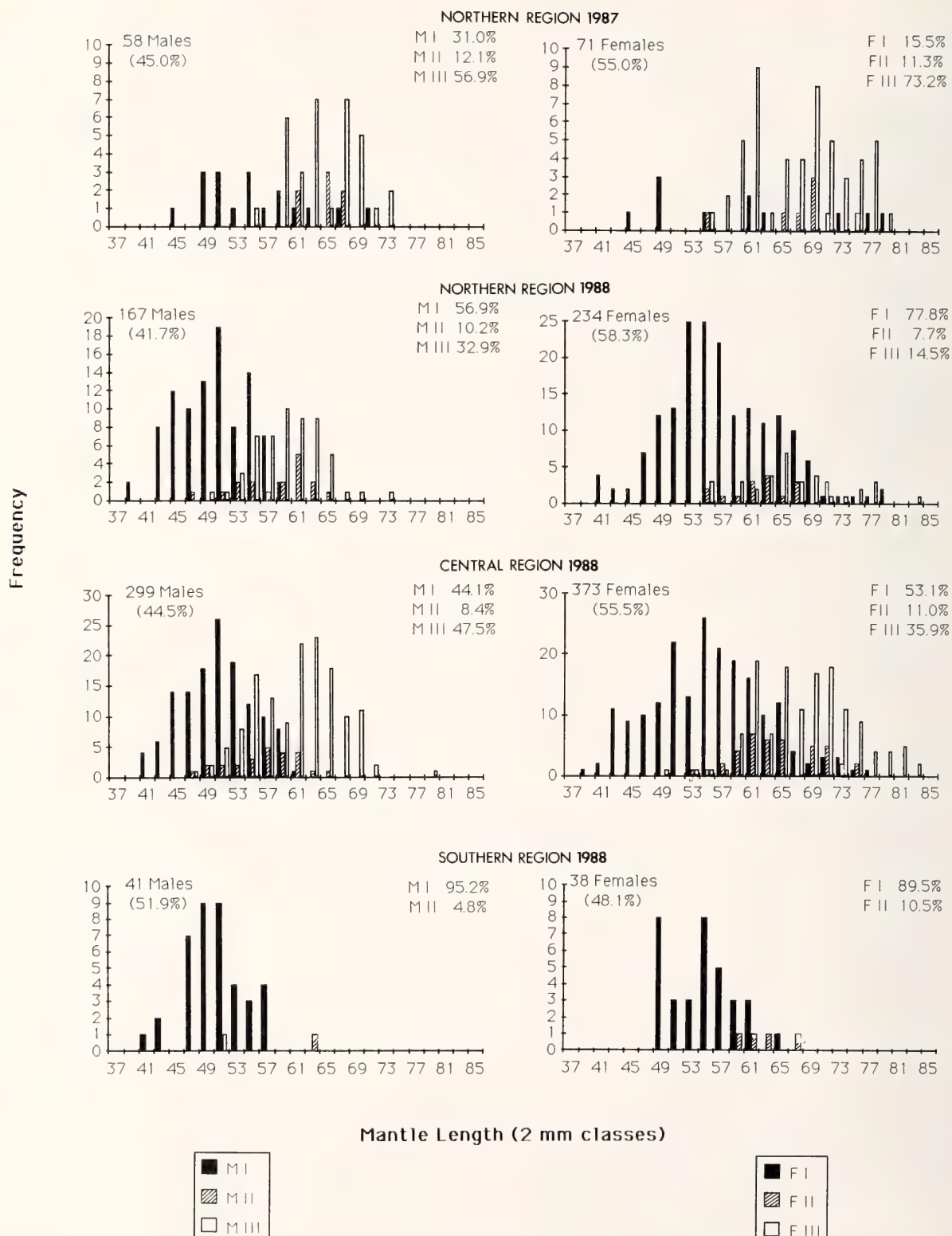


Figure 5

Sepia australis maturity stages: frequency of occurrence compared in successive years off the west coast in summer (1987-1988) in the northern region and by region in 1988. Sample size and percentage of each sex are indicated for each region. M—males; F—females.

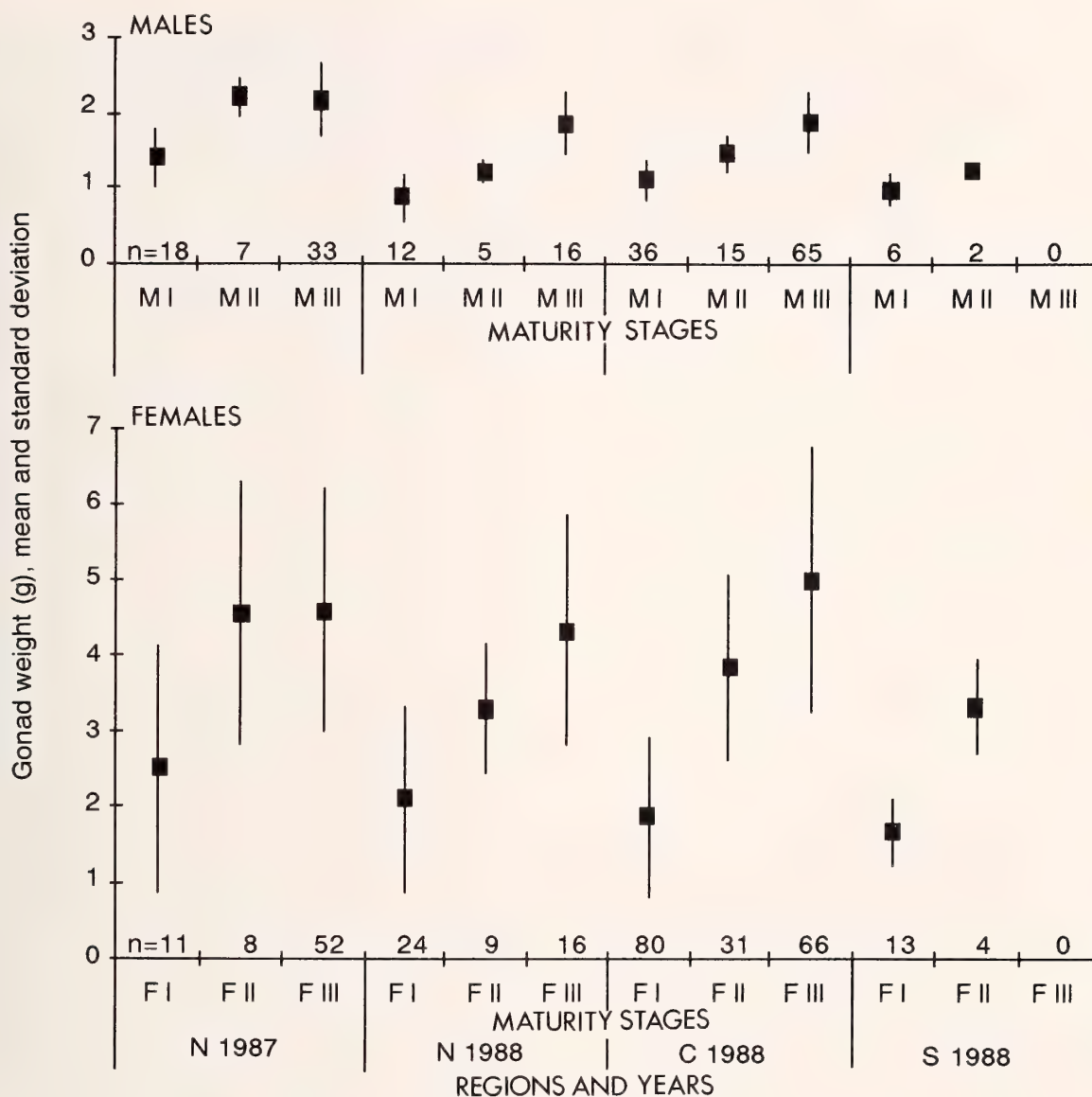


Figure 6

Mean gonad weight and standard deviation for *Sepia australis* by maturity stage and by region in summer 1987 and 1988, off the west coast of southern Africa.

southern Africa lies close to 27°00'S in Namibian waters, as established by SANCHEZ & VILLANUEVA (1989). They reported fairly high concentrations of this species, but the units of measure (individuals per mile) are unfortunately not comparable with those presented here. However, their report of a consistently high abundance of *S. australis* is in accordance with our observations of its great abundance and importance in the Benguela ecosystem (Figure 2; LIPINSKI *et al.*, 1991). The main concentrations of *S. australis* are located between St. Helena Bay and Elizabeth Bay, south of Lüderitz (SANCHEZ & VILLANUEVA, 1989, 1991; Augustyn *et al.*, unpublished data; our data). Its distribution seems to be fairly uniform in the 100–209 m depth

zone (our data; Augustyn *et al.*, unpublished data; SANCHEZ & VILLANUEVA, 1989, 1991).

The white-chinned petrel (*Procellaria aequinoctialis*) seems to be an important consumer of *Sepia australis*, as most of the Sepioidea reported from the gizzards and stomachs of these birds by JACKSON (1988) probably belonged to this species (Lipinski, unpublished data). The white-chinned petrels, however, most probably scavenge dead *S. australis* from the sea surface (LIPINSKI & JACKSON, 1989) and therefore the abundance of the birds does not influence the abundance of *S. australis*.

The Cape hake is the most important predator of *Sepia australis* identified to date (LIPINSKI *et al.*, in press); yet

there seems to be no link between the changes in abundance of these two species (Figure 2A, B). On the other hand, existing data show parallel changes in abundance for *S. australis* and *Pterygosquilla a. capensis* for at least six trawl surveys (see results of Fisher's Exact Probability Test), which suggests that these two species may respond similarly to biological or environmental factors, or some combination of these. It is unlikely that these changes reflect predator-prey interactions because there is no time lag (Figure 2A, B), as predicted by the classical Lotka-Volterra model and its more sophisticated modifications (e.g., BEGON & MORTIMER, 1981:119-128).

The interaction between *Sepia australis* and its other important prey species, the lightfish *Maurolicus muelleri*, cannot be assessed at present. Data for *M. muelleri* are scarce and difficult to interpret (M. Armstrong, personal communication). It would seem, however, that the lightfish also shows seasonal (summer-winter) fluctuations; concentrations in summer have a higher density, especially in the Cape Columbine area (ARMSTRONG & PROSCH, 1991).

The trends in the abundance of *Sepia australis* reported here are essentially in agreement with the biomass estimates found by Augustyn *et al.* (unpublished data). In addition, there were regional differences (Figure 3A, B), and catches (kg/trawl) were much higher in the northern and central regions than the overall mean value for the entire survey (Table 1).

This assessment of abundance for *Sepia australis* is almost certainly an underestimate of total *S. australis* biomass, because of the sepiid's small size, and the relatively large mesh size in the cod end. The catchability coefficient of *S. australis* must be very different from that of hake, the main target species in the biomass surveys. This suggests that the abundance of *S. australis* is far greater than reported here and by Augustyn *et al.* (unpublished data).

Population Structure

Both length and weight of *Sepia australis* seem to vary from year to year in the central 1 and northern regions. Animals from the southern region are, however, very different (Table 2): they are much smaller and show less variation (smaller standard deviations). This is in agreement with the data for the south coast (at a different time of year, May 1988), where most of the *S. australis* were sexually maturing or mature (Roeleveld *et al.*, unpublished data).

For the squid *Todarodes pacificus*, the length-weight relationship has been found to be an important indicator of stock conditions (biological characteristics and stock identity) in various areas and different years (MURATA, 1978). The length-weight relationships in *Sepia australis* were found to be similar in slope and intercept for both sexes and within each sex between years and regions, except in the southern region in 1988 (Figure 4). This similarity (especially between sexes) agrees with observations of ROELEVELD (1972:278) and SANCHEZ & VILLANUEVA (1991), and was also reported by BELLO (1988) for *S.*

orbignyana and *S. elegans* in the southern Adriatic Sea. This similarity, however, may well have been the result of the relatively uniform size within the samples investigated as well as the small data sets available.

The analysis of maturity stages revealed considerable variation between years and regions. The general characteristics of the animals from the southern region in 1988 most resemble those of animals off the south coast (Roeleveld *et al.*, unpublished data) but differ in maturity. Most of the *Sepia australis* off the south coast in May 1988 were either maturing or fully mature (Roeleveld *et al.*, unpublished data); near Cape Point (34°18'S, 18°30'E) in February 1988, most of the specimens were immature (Figure 5). This difference in maturity may be attributed to the three-month time difference.

On the other hand, animals from the southern region differed considerably from those of the northern and central region in abundance, sex ratio, mean length and weight, length-weight relationship, and distribution of maturity stages. All these biological differences indicate that *Sepia australis* off the south coast may belong to a separate population.

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NOTES, INFORMATION & NEWS

Seasonal Abundance of the Small Tropical Sepioid *Idiosepius pygmaeus* (Cephalopoda: Idiosepiidae) at Two Localities off Townsville, North Queensland, Australia

by

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Large numbers of the small tropical sepoid *Idiosepius pygmaeus* Steenstrup, 1881, were discovered recently in near-shore and estuarine habitats in North Queensland, Australia, including along the breakwater systems of the Townsville harbor and marina complex (JACKSON, 1989), but because of the littoral habitat of *I. pygmaeus*, individuals could not be sampled with towed nets. Due to their dark pigmentation and neustonic behavior, individuals of *I. pygmaeus* could be easily observed and dip-netted by walking along the breakwaters. A visual census technique was therefore used to determine trends in abundance throughout the year. The sepoids collected during the regular sampling episodes were used both for length-frequency analysis and for discerning any seasonal patterns in growth (see JACKSON & CHOAT, 1992). This paper reports the results of the visual census technique for monitoring the relative abundance of *I. pygmaeus* at two localities in the Townsville region of North Queensland.

Both visual and dip-net census techniques were incorporated to monitor changes in the numbers of *Idiosepius pygmaeus* through time. The study sites were two breakwater systems located within 2 km of each other on each side of the Townsville harbor (19°15'S, 146°50'E), which lies within the central Great Barrier Reef province. Although the region is tropical, there is a considerable seasonal fluctuation in water temperature. Surface water temperatures just offshore from Townsville fluctuate between 19.3°C and 30.9°C, with the summer maximum in January and the winter minimum in July (WALKER, 1981). The Townsville western breakwater/marina complex was used for visual monitoring, which consisted of walking along 3.2 km of breakwater and noting the presence of any individuals of *I. pygmaeus*. The sepoids were left undisturbed except for a few individuals collected on several occasions for aquarium experiments. Counts were taken approximately monthly from July to December 1987 and then generally fortnightly throughout 1988 and 1989.

The Townsville eastern breakwater complex was the

site of regular collections of *Idiosepius pygmaeus* for the study of seasonal variation in growth. All individuals observed were dip-netted along approximately 1.72 km of the breakwater. The sample was obtained by pooling all individuals captured from paired collecting trips, which usually consisted of an afternoon trip followed by one the next morning. Each sample usually consisted of both a low- and high-tide collection. The distance covered during one visual census taken on the western breakwater (3.21 km) was roughly equivalent to the distance covered on the paired sampling trips along the eastern breakwater (3.44 km; i.e., 1.72 km × 2 trips).

On the basis of visual counts at the western breakwater, the abundance of *Idiosepius pygmaeus* varied considerably, with periods of high abundance interspersed between periods of absence or very low abundance (Figure 1). Generally, very few individuals were observed over the summer months (December to February) during all three years. This pattern is even more accentuated if the total abundance from collected specimens on the eastern breakwater is superimposed over the western breakwater visual census (Figure 1).

Because sampling was generally taken on alternate weeks at the two breakwaters, monthly abundances are difficult to compare directly. However, during comparable periods, the pattern in abundance was similar at the two breakwaters: for example, the drop in *Idiosepius pygmaeus* abundance during October–November, followed by a subsequent rise in abundance during February 1989. The pattern in abundance for both breakwaters also was similar during the period between July and November 1989. This suggests that *I. pygmaeus* on both breakwaters is responding in a similar way to some external environmental factor influencing abundance.

Although most reports of temperate *Idiosepius* species indicate preference for a benthic/seagrass habitat (SASAKI, 1923; BURN, 1959), *Idiosepius pygmaeus* appears to be predominantly free swimming and littoral. The distribution of *I. pygmaeus* in shallow water along the Townsville breakwaters bears a close resemblance to the habitat description given by MOYNIHAN (1983:44) for Koror, Palau, in which individuals were captured in shallow water (less than 1 m depth) "over hard and rather bare surfaces, natural rock and coral or artificial concrete and iron" and "floating or swimming high in the shallows near the shoreline on bright sunny days." *Idiosepius pygmaeus* in Australia was observed most commonly at the surface, and even after considerable disturbance (e.g., missing them with a dip-net) they usually returned to the surface after 1 to 5 min.

The regular absence of *Idiosepius pygmaeus* in inshore waters during warm periods is not yet fully understood.

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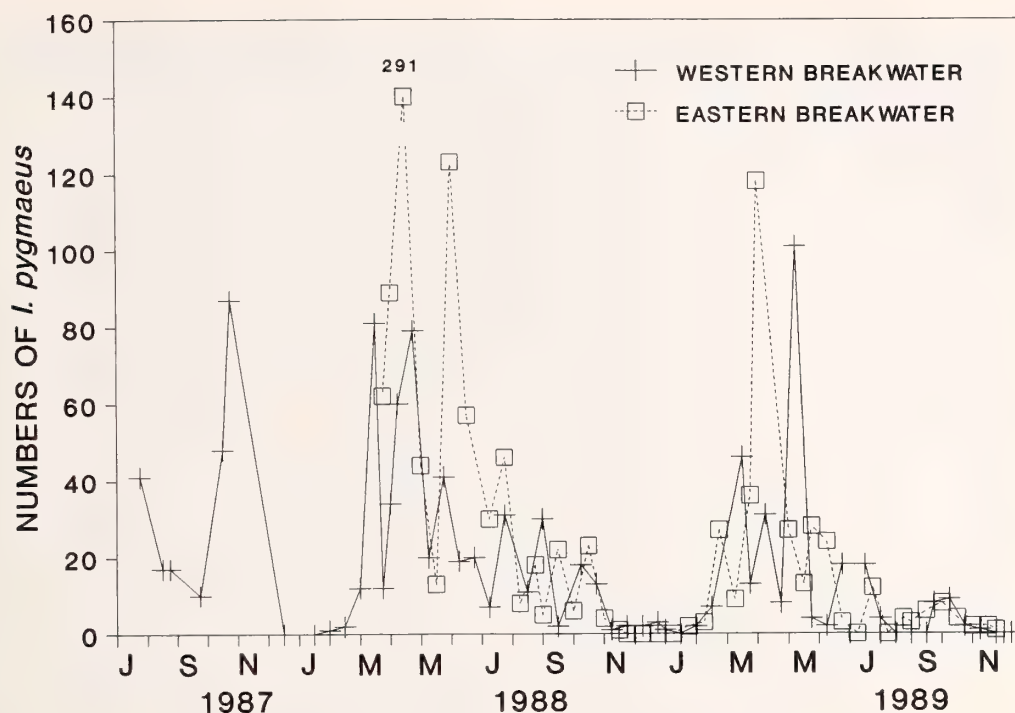


Figure 1

Numbers of individuals of *Idiosepius pygmaeus* collected along the eastern breakwater and counted along the western breakwater/marina complex. Note that the peak in March 1987 for the eastern breakwater (291 individuals) is not drawn to scale.

Idiosepius pygmaeus has been caught in considerable numbers at night around light traps in 22 m of water, 500 m off Lizard Island (a continental island, northern Great Barrier Reef waters) in early January (McCormick, personal communication) while they are virtually absent from the breakwater habitat at Townsville. The close association of *I. pygmaeus* with surface waters may be one factor constraining its temporal distribution along the breakwaters. High surface water temperature may force *I. pygmaeus* to migrate to deeper waters, but since this sampling regime was visual, movement into deeper water would not be detected. Also, juvenile fish were particularly abundant along the breakwaters during the summer periods, and may have increased predation pressures on *I. pygmaeus* during that period. *Idiosepius paradoxa* in Japan is a prey item for the lancetfish *Alepisaurus ferox* (KUBOTA & UYENO, 1979). Although *I. pygmaeus* feeds predominantly on the inshore sergestid shrimp *Acetes sibogae australis*, which often swarms along the breakwater systems (unpublished data), preliminary monitoring of the seasonal abundance of *Acetes* did not show any relationship to the seasonal abundance patterns of *I. pygmaeus* (JACKSON, 1991).

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***Conus striatus* Survives Attack by
Gonodactyloid!**

by

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Gonodactyloid crustaceans (members of the order Stomatopoda) are masterful predators of gastropod mollusks, despite the strong, protective shells of their prey. To access the gastropod's soft body, they use highly modified second thoracopods in a remarkably diverse array of shell-fracturing techniques. These include breaking off the shell apex, holding the shell against the home burrow wall and breaking shell away from the outer lip, and punching a large (5–25-mm across) hole in the dorsum of the shell (CALDWELL & DINGLE, 1976; GEARY *et al.*, 1991).

GEARY *et al.* (1991) document such holes in Recent shells and argue for stomatopods of the genus *Gonodactylus* and related genera as the cause of similar holes in Pliocene and Pleistocene fossil shells belonging to several prosobranch families. They reported holes of this type most frequently in Strombidae, and search of fossil collections and illustrations in the literature will likely reveal additional examples. A hole that appears to be about 16 mm across in a Pliocene specimen of *Tylospira*, in the stromboidean family Struthiolariidae, was recently illustrated (DARRAGH, 1991).

Gonodactylus and its relatives punch holes in shells by using the base of the dactylus, which is enlarged, hemispherical, and heavily calcified, forming a structure analogous to the ball peen of a hammer head. "With this appendage, stomatopods can punch through crab carapaces, mollusc shells, echinoderm tests, Erlenmeyer flasks, and even the walls of aquaria" (GEARY *et al.*, 1991). I have occasionally observed empty, often worn shells of Recent *Conus*, particularly *C. striatus* in Hawaii, with such holes. It was only upon reading the report by GEARY *et al.* (1991) that I understood their likely cause. Of course in the absence of direct observation, the possibility remains of an agent other than a gonodactyloid.

Here I report that attacks on gastropods apparently due to gonodactyloids are not inevitably fatal. This is demonstrated by a singular specimen of *Conus striatus* that not only survived such an attack but lived to repair the damage to its shell. It recorded the event by a resulting shell scar of a type that to my knowledge has not previously been

reported to occur in nature, and it likely grew by further shell accretion before it was killed and collected by a specimen of *Homo sapiens*.

Observations

The specimen (Figure 1), in the Staatliches Museum für Naturkunde, Stuttgart (SMNS), is 76 mm long and 37 mm in maximum diameter. It was collected at Ranong, Thailand, by A. J. da Motta. The shell has about 11 postnuclear or teleoconch whorls. The maximum dimensions of the hole are 23 mm in the shell's axial direction and 19 mm normal to the axis of coiling. It is located in the last whorl, from about 120° to about 185° back from the outer lip or growing edge of the shell when the animal died.

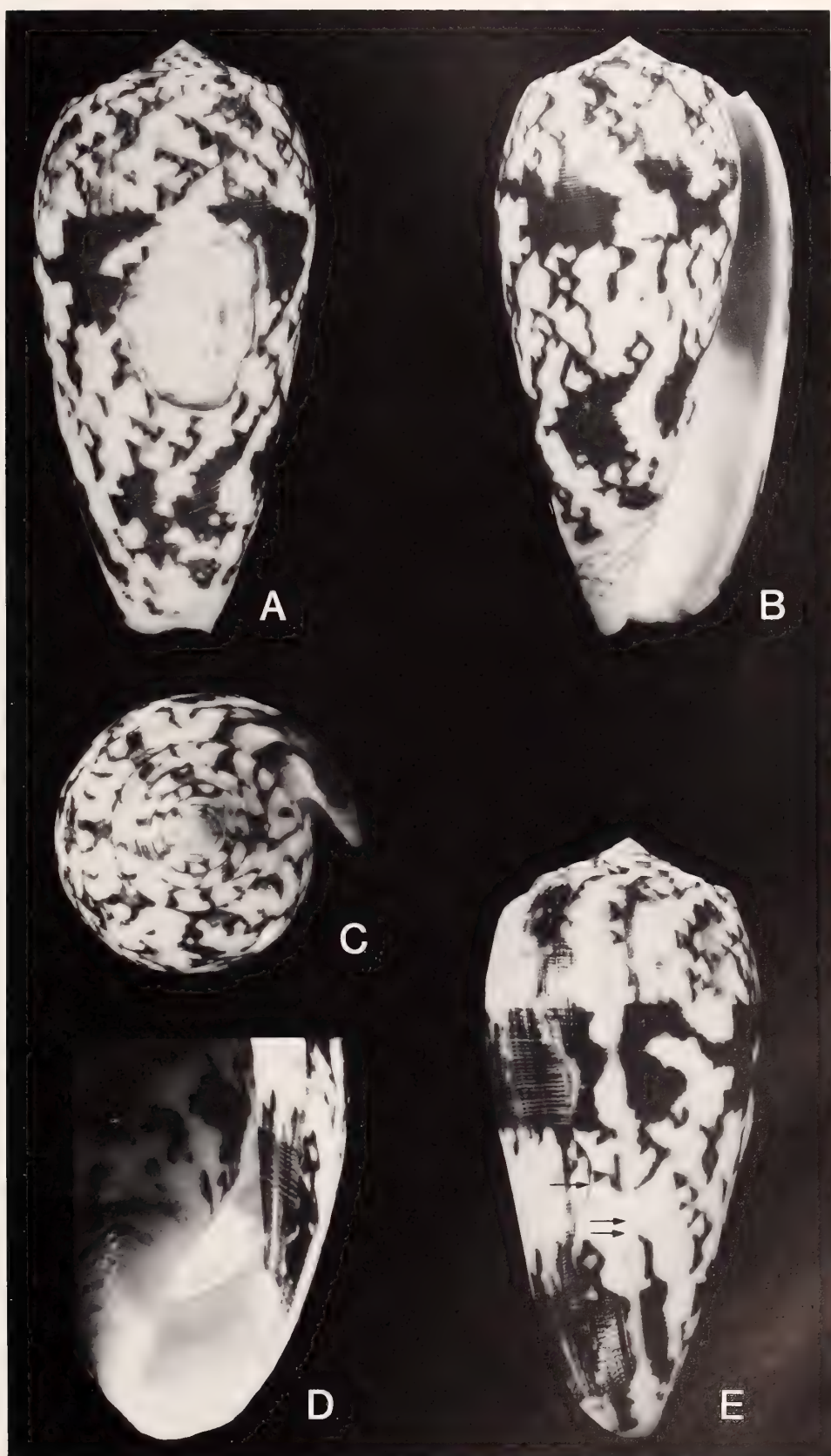
The hole was filled by shell material that differs in appearance from the general surface of the normal shell. The outermost layer of normal shell, referred to as layer 1 (KOHN *et al.*, 1979), is usually relatively thin (about 0.6 mm or about 20–25% of total shell thickness in a *Conus striatus* shell of the size under consideration). Most likely, the hole was filled by shell material secreted by those regions of the mantle responsible for the thickest and strongest middle layer (layer 2) and the inner layer (layer 3) (KOHN *et al.*, 1979; CURREY & KOHN, 1976).

The inner surface of the shell is quite smooth under the repair scar, indicating participation of layer 3 in its secretion. On the outer surface of the scar, the shell material is mostly white but contains some irregular brown pigment blotches. The brown pigment in the normal shell along the edge of the hole appears to be in layer 1 and perhaps the outer portion of layer 2. A narrow peripheral band of outer mantle epithelium normally secretes the outermost shell layer (layer 1) (WILBUR & SALEUDDIN, 1983). The absence of its participation in the repair process away from the shell edge may explain the near absence of pigment in the scar.

The crystal architecture of the regenerated shell is unknown, as this could not be determined non-destructively. All layers of normal *Conus* shell are of crossed-lamellar aragonite (KOHN *et al.*, 1979). In other mollusks, repaired shell away from shell edges often differs in structure from normal shell. When repairing such breaks, terrestrial pulmonates replace crossed-lamellar shell with other fabrics, but the only prosobranchs studied, the freshwater meso-

Figure 1

Conus striatus Linnaeus, illustrating shell repair following attack attributed to gonodactyloid stomatopod. Specimen from Ranong, Thailand, in SMNS. 76 × 37 mm. A. Dorsal view, showing entire repair scar. B. Ventral view. C. Posterior or apical view, showing absence of shell repairs on shoulders of earlier whorls. D. View into aperture from anterior end, with repair scar (light area) illuminated from below. E. Right laterodorsal view; shell rotated to show jagged collabral repair scar (single arrow) and smooth, collabral line possibly indicating temporary cessation of growth (double arrow).



gastropods *Viviparus* and *Pomacea*, replace crossed-lamellar with crossed-lamellar shell (WATABE, 1983).

Although the repair scar I describe here is marked with about 15 growth lines (Figure 1A), it is difficult to discern where it was initiated. The growth lines at the distal limit of the hole (*i.e.*, nearest the outer lip) are small and arcuate, and they overlie the larger, more proximal lines. Because the inner mantle surface may secrete shell material readily only under previously deposited shell, the most likely sequence of filling of the hole is thus distal to proximal. However, it is possible that repair along the longer, proximal lines that parallel the irregular outline of the hole was also initiated at the onset of repair, and that subsequent episodes of parallel shell secretion abutted or slightly overlapped the earlier shell. Reconstruction initiated from all sides or exclusively from the distal point would likely expose the soft mantle tissue maximally to the environment during the process. However, such exposure may stimulate shell regeneration over the entire exposed mantle (WATABE, 1983).

The edges of the repair scar were not filled, so the outside is not flush with the surrounding undamaged shell. This is expected if the repair occurred from the inside by a skirt of mantle tissue too stiff to conform to the edge of the hole.

In addition to the repair of the putative stomatopod hole, the *Conus striatus* shell bears a jagged repair scar about 3–10 mm (about $\frac{1}{8}$ whorl or 45°) back from the outer lip and generally parallel to it (Figure 1E). It is not possible to ascertain whether this scar occurred before, during, or after the stomatopod attack, or even whether it was caused by a crustacean. However, several aspects suggest that it too could be an outcome of the unsuccessful gonodactylid attack: (1) Using their 3rd–5th thoracopods, often called maxillipeds, gonodactylids sometimes wedge their prey against the burrow wall while hammering (CALDWELL & DINGLE, 1976); this could cause damage all along the thin outer lip of the shell. (2) The pattern of concave breaks 7–8 mm long (Figure 1E, single arrow) is not inconsistent with the effect of hammering by a gonodactylid dactylus. (3) The color pattern of the shell changes abruptly at this scar. The characteristic brown spiral lines (for which Linnaeus named the species) become more distinct, and generally less pigment is deposited, in shell material secreted after this event (Figure 1E). That this suggests a traumatic experience is supported by two lines of anecdotal evidence. I have frequently observed changes in color pattern in shell secreted after repair of outer lips broken in unsuccessful attacks on *Conus* by crustaceans. And I have seen similar pattern shifts in *C. striatus* transported from Guam to Seattle and subsequently fed fishes from Puget Sound (Cottidae) rather than their native diet. If this interpretation is correct, the shell removed in the attack would have been about 75–135° from the outer lip at the time of injury.

On the other hand, there is in the specimen reported here a smooth collabral line about 15 mm back from the outer lip (Figure 1E, double arrow)—*i.e.*, earlier in the

animal's life than the repaired lip just described. The white ground color of shell deposited proximal to this line is densely but irregularly suffused with pink; thereafter, pink pigmentation is sparse, both before and after the jagged collabral scar. This line could possibly indicate the position of the outer lip at the time of the attack, but its uniformity suggests that it represents a growth cessation rather than a response to injury.

Following discovery of the shell described here, I examined the entire collection of *Conus striatus* in the SMNS ($n = 107$, most also collected by Mr. da Motta) for evidence of shell repairs following attempting predation. I found no other evidence of stomatopod attacks. Three of the 30 additional specimens from western Thailand had repair scars on the last whorl, as did 3 of 76 from other localities throughout the tropical Indo-Pacific region (one each from Samoa, Fiji, and Réunion). These were likely due to attacks from crabs, but this cannot be determined with certainty. The average number of 0.06 repairs per last whorl in *C. striatus* is lower than in most other species surveyed. VERMEIJ (1989) found an overall mean of 0.29 but with wide variation (range 0–1.0; SD 0.25) in 59 samples of 14 other Indo-Pacific *Conus* species. In two samples of *C. striatus* in the B. P. Bishop Museum, Honolulu, from Guam ($n = 14$ shells) and Maui ($n = 15$ shells), VERMEIJ (*in litt.*) noted averages of 0.3 and 1.3 repair per shell, respectively (overall average 0.8).

Discussion and Conclusion

Marine gastropods frequently repair damage to the outer shell lip following unsuccessful predation attempts (*e.g.*, VERMEIJ, 1987), but repair of mid-shell holes is poorly documented and appears to be rare, in contrast to the case in some terrestrial and freshwater forms (WATABE, 1983). Adult *Conus* frequently survive attacks by crabs that attempt to peel off the outer lip but are unable to break the thicker, multi-layered shell farther back. In the direction that the crab claw must apply force (normal to the length of the outer lip), the primary lamels of layer 1 may be pulled apart from each other. However, layer 2 is nearly twice as thick, and its crystals are oriented so that the tightly packed secondary lamels or laths would have to be broken across their long axes. Because of these architectural features, the crossed-lamellar structure of *C. striatus* is highly anisotropic. Its bending strength in the direction of attempted breakage is about 200 MNm⁻² but only about 70 MNm⁻² in the direction at right angles to this. This enables the animal to survive by withdrawing into the shell beyond the limit that the crab can break. It later repairs the shell, leaving a record of the unsuccessful predation as a scar (CURREY & KOHN, 1976).

Several factors probably allowed the unusual instance reported here of survival of a gastropod following severe damage to the shell in the form of a large hole punched some distance from the outer lip during a presumed sto-

matopod attack; all remain speculative but are amenable to experimental test. Whether or not the predator was itself preyed upon or otherwise driven away while subduing the *Conus* is of course unknown. It is unlikely that the *Conus* retaliated by stinging the predator, because the *Conus* venom apparatus is an offensive, not defensive weapon system, and *C. striatus* in particular usually responds to handling by withdrawal into the shell, not by extension of the proboscis. If the attempted predation was simply unsuccessful, it is unlikely that the *Conus* had eaten recently. Because *C. striatus* kills and swallows large fishes whole, its foregut is often distended for some hours after feeding (Kohn, 1956). This prevents retraction of the body within the shell and probably would have rendered the *Conus* completely susceptible to predation by the stomatopod without shell breakage. In this case, however, the *Conus* may have been able to withdraw the mantle and body within the shell beyond the position of the stomatopod's hammering activities, so that they did not damage its soft tissues. In this case a typical gastropodan outlook on life—when danger threatens, withdraw into your shell; things will improve by and by—appears to have served *Conus striatus* well and to have caused the “thug of crustaceandom” (Schmitt, 1965) to meet its match.

Acknowledgments

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- Case 2526—*Strombiformis albus* Da Costa, 1778 (currently *Melanella (Balcis) alba*; Mollusca, Gastropoda): proposed conservation of the specific name.
- Opinion 1676—*Lepidomenia* Kowalevsky in Brock, 1883 (Mollusca, Solenogastres): *Lepidomenia hystrix* Marion & Kowalevsky in Fischer, 1885, designated as the type species.
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- Opinion 1678—*Helicarion* Férussac, 1821 (Mollusca, Gastropoda): conserved, and *Helicarion cuvieri* Férussac, 1821, designated as the type species.
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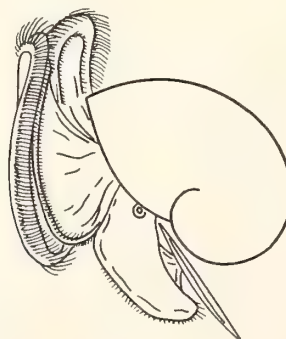
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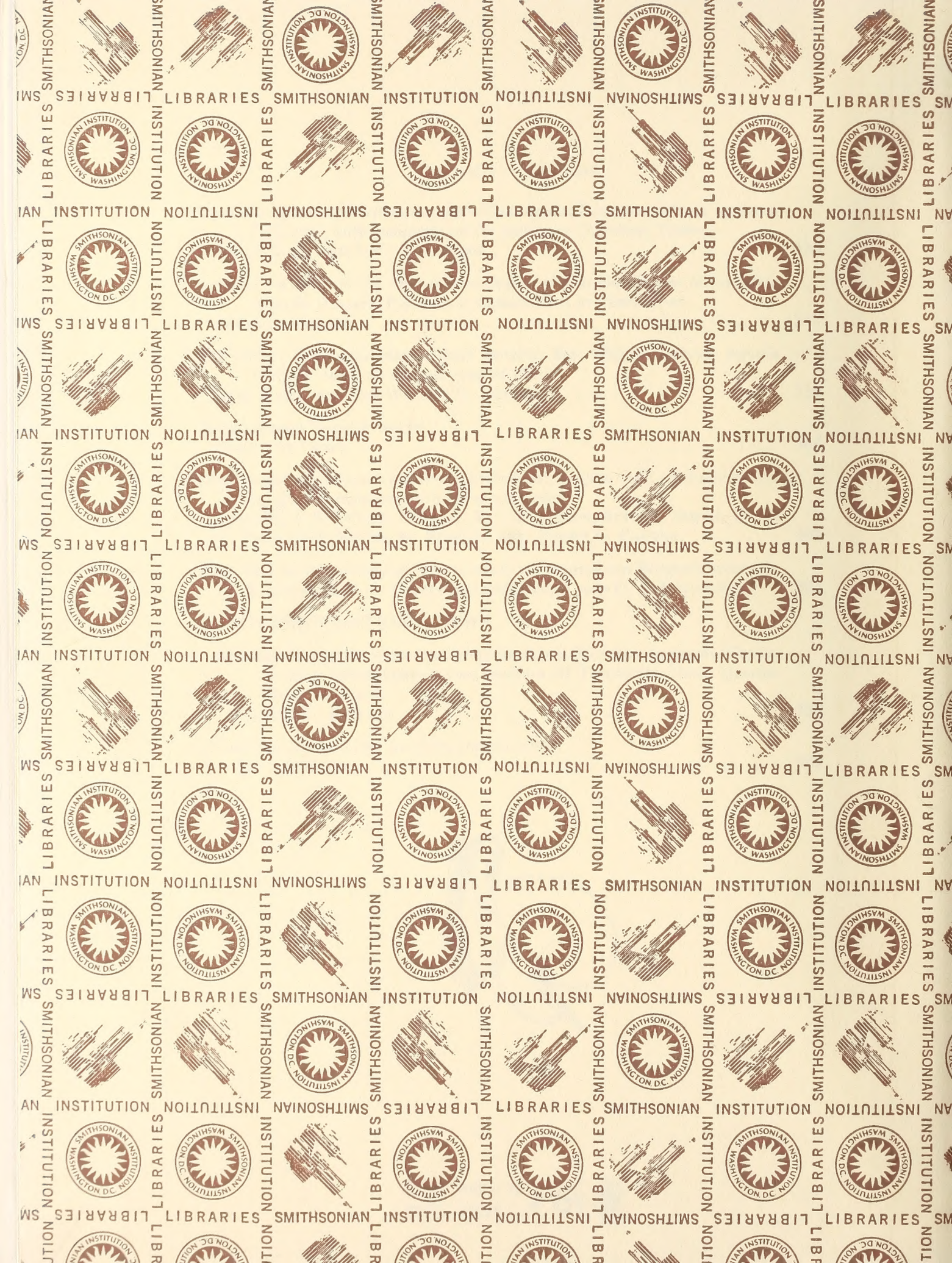
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